

# North Sapphire Elk Research Project

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## Executive Summary

The elk (*Cervus canadensis*) population in the northern Sapphire Mountains of west-central Montana has increased approximately 350% since the 1960s. Recent estimates have exceeded Montana Fish, Wildlife and Parks (MFWP) management objectives for population size. In response, more liberal antlerless harvest regulations have been implemented to reduce population size. However, extended elk use of lower-elevation private lands with restricted public access may limit the effectiveness of harvest regulations in reducing female elk survival rate and reducing population size. Additionally, the current distribution of elk remains a concern to some landowners trying to prevent agricultural or property damage, to the hunting public finding fewer elk present on public lands during the general hunting season, and to biologists trying to manage the population through general hunting season regulations. In response to these concerns, MFWP and partners initiated the North Sapphire Elk Research Project to better understand public perception regarding elk and elk management and to collect baseline biological data on elk habitat and movements.



The study area included the northern Sapphire Mountains and the northern Bitterroot Valley, primarily located in hunting district (HD) 204. Lower elevations primarily consisted of privately-owned residential and agricultural lands adjacent to grass- and shrub-dominated mountain foothills and a riparian corridor along the Bitterroot River in the valley bottom. Higher-elevation mountainous areas primarily consisted of publicly-owned conifer forests in a variety of successional stages due to past timber harvest and wildfire activity.

To understand public perceptions of elk populations, hunting regulations, and hunting access, we surveyed 1,829 resident elk hunters and 33 private landowners residing in HD 204. The majority of both groups responded that elk numbers appear lower than desirable and that there appear to be fewer elk now as compared to the past. Wolves, high hunting pressure, predators in general, and weather/climate change were the most frequently mentioned reasons for the lower elk numbers reported by both groups. Despite this perception of low elk numbers, the majority of both groups reported general satisfaction with current elk regulations and management in HD 204. Survey results also demonstrated that public access to hunt elk on private properties in HD 204 may be limited given the large proportion of landowners that allow hunting primarily to family or friends and do not use a Block Management system.

To gain insight into elk population status and distributions, we sampled and radio-collared 48 female and 28 male adult elk during February 2014 and 2015. Collars remained on



the animals until February 2016. The annual survival rate was 0.91 (95% confidence interval [CI] = 0.82–0.96) for adult females and 0.46 (95% CI = 0.26–0.64) for adult males. The primary source of mortality for female (71%) and male (87%) elk was harvest-related (i.e., harvest or wounding loss), and we observed no confirmed predation events during the 2-year study. We identified annual and seasonal ranges of female and male elk based on GPS collar locations. Female annual ranges generally occurred at lower elevations than males and consisted primarily of private land ( $\bar{x}$  = 62%). Female elk were most widely distributed during the calving and summer season and were more concentrated during hunting seasons at lower elevations, primarily on private land. Male elk were most widely distributed during the archery season but became more concentrated at lower elevations during the rifle and winter-spring seasons. During the archery season, female and male elk ranges were composed on average of 44% and 53% public land, respectively. During the rifle season, female and male elk ranges were composed on average of 30% and 48% public land, respectively.



We found that migration strategies varied within the population, with 25% of female classified as residents, 27% as migrants, and 48% as intermediate behaviors that lie somewhere between residency and migration. We found that each migratory strategy was exposed to different qualities of forage during summer, and forage quality exposure decreased along the continuum of behaviors from residency to migration. Irrigated agricultural areas with high forage quality contributed strongly to these nutritional differences; resident elk were located in irrigated agricultural areas for 10 more days during summer than intermediates and 24 more days than migrants. Differences in available nutritional resources have strong potential to influence elk distributions and migratory behaviors. Changing or decreasing migratory behaviors may affect natural ecosystem processes and may result in increasing property damage issues on private lands and lack of elk availability on public lands during the fall hunting season.

Increased elk use of lower-elevation private lands in the North Sapphire area limit the effectiveness of traditional public hunting strategies to maintain the North Sapphire elk population within objective levels. Our results suggest that strategies integrating management of habitat quality, hunter access, and hunting regulations that are matched to the migratory behaviors present in the population may be useful for elk managers. We suggest that elk and forest managers working in collaboration may be able to enhance nutritional resources for migratory elk and encourage resident elk to use forested areas. Developing strategies to balance hunter pressure across the landscape by alleviating public hunting restrictions on private property through collaboration with private landowners and by reducing hunter pressure on public lands are ultimately essential for redistributing more elk onto public lands and reducing the elk population to within population objectives.

## Section 1 — Introduction



Elk (*Cervus canadensis*) studies across Montana and the greater Yellowstone area have strengthened our understanding of the factors influencing elk populations, habitat selection, and distributions. Understanding the variable responses of elk to different landscape and ecosystem conditions, including, for example, carnivore communities (White and Garrott 2005, Garrott et al. 2008, Proffitt et al. 2009, 2014, 2016a, 2016b), distribution and availability of nutritional resources (Cook et al. 2004, Middleton et al. 2013, Proffitt et al. 2016a, 2016b), and the amount and distribution of publicly accessible lands for hunters (Proffitt et al. 2013, 2016c) has provided valuable information to inform elk management decisions. In most elk populations, including those in Montana, hunter harvest is the greatest cause of adult elk mortality and can cause redistribution of elk populations during the hunting seasons (Irwin 2002, Skovlin et al. 2002, Proffitt et al. 2010, Brodie et al. 2013). As a consequence, there is evidence that elk are increasingly inhabiting lands with restricted public hunting access, which can limit traditional hunter harvest as a management tool for maintaining populations within population objective levels (Burcham et al. 1999, Haggerty and Travis 2006, Proffitt et al. 2010, 2016c).

While elk survival may be enhanced by elk use of properties with restricted hunter access, there may be consequences to reproduction and long-term survival depending on the availability and quality of nutritional resources accessible to elk in these refuge areas (Cook et al. 2004, 2016). The late summer and fall period, during which Montana's hunting seasons occur, is of particular importance for adult female elk to replace mass loss from the previous winter, build fat reserves to survive the winter, support lactation, and establish pregnancy (Cook et al. 2004, 2016, White et al. 2011, Proffitt et al. 2016a). Typically, heterogeneous landscapes of grasslands, shrublands, and multi-successional stage coniferous forests provide adequate resources and fulfill biological requirements for elk (Lyon and Jensen 1980, Skovlin et al. 2002). However, elk that are redistributed to properties with restricted hunter access due to hunting activities may be constrained by limited access to the nutritional resources provided in traditional habitats. Alternatively, these properties may provide both security from harvest and easily accessible, high quality nutritional resources that meet elk physiological and reproductive nutritional requirements.

Elk in the northern Sapphire Mountains of west-central Montana occupy a diverse landscape that has been modified by human activities. Adjacent to the Bitterroot River are gallery cottonwood forests and riparian habitats flanked by grassland and shrubland habitat that provide important winter range for elk. Land conversion and development in these low-elevation habitats has increased in recent decades and has created a matrix of housing developments and

agricultural areas. Higher elevations consist of extensive coniferous forests and provide summer range for elk. Intensive timber harvest throughout the northern Sapphire Mountains during the mid- to late-1900s and historic wildfires of varying frequencies and intensities have created heterogeneous forests in various successional stages. While timber harvest on public lands in the Bitterroot Valley decreased 70% during 1980-2013 (U.S. Department of Agriculture, Forest Service 2016), wildfire activity has continued to increase due to decades of fire suppression and fuel accumulation (Stephens and Ruth 2005, Dennison et al. 2014). Wildfire now represents the primary disturbance in coniferous forests of the Bitterroot Valley (Gibson et al. 2014) and may have important consequences to elk populations by altering the distribution and availability of nutritional resources across the landscape (Rowland et al. 1983, Hobbs and Spowart 1984, Cook et al. 2004, 2016, Van Dyke and Darragh 2006, Greene et al. 2012, Proffitt et al. 2016a).

The North Sapphire elk are an important part of the region's natural and human landscape. These elk provide hunting and viewing opportunities to residents of the Bitterroot and Missoula Valleys, as well as visitors from outside the region. The elk population has been managed for harvest opportunities for several decades by Montana Fish, Wildlife and Parks (MFWP). The elk population was at historical recorded lows of about 200-250 individuals through the 1960-1970's but



began increasing in the late 1980's. The highest population count occurred in 2004 at 1,019 elk, and subsequently, MFWP increased hunter opportunity that effectively reduced the population to within elk objective numbers. Under more restrictive hunting regulations, the population peaked again in 2016 at 990 elk and has remained above objective numbers for the past three years. During the hunting seasons, elk have increasingly used low-elevation private lands with restricted public hunting access. This movement has limited the effectiveness of more liberal antlerless harvest regulations to reduce the population. Some of these private properties, notably irrigated agricultural areas and substantial parcels of restored rangelands, are attractive to elk not only for the security provided during the hunting season but also for the availability of high quality forage. The extended valley habitation and use of restricted public access properties by elk is undesirable to some landowners trying to prevent agricultural or property damage, to the hunting public facing reduced hunter opportunity from inaccessible elk, and to biologists trying to manage the population through traditional and typically effective public hunting methods (Haggerty and Travis 2006).

A growing concern within the North Sapphire elk is the potentially increasing use of low elevation, privately-owned winter range year-round. Typical elk migration strategies entail movements from lower elevation grassland and shrubland wintering range to higher elevation summer range in coniferous forests (Irwin 2002, Skovlin et al. 2002). The extensive coniferous forests in the northern Sapphire Mountains in a variety of successional stages provide im-

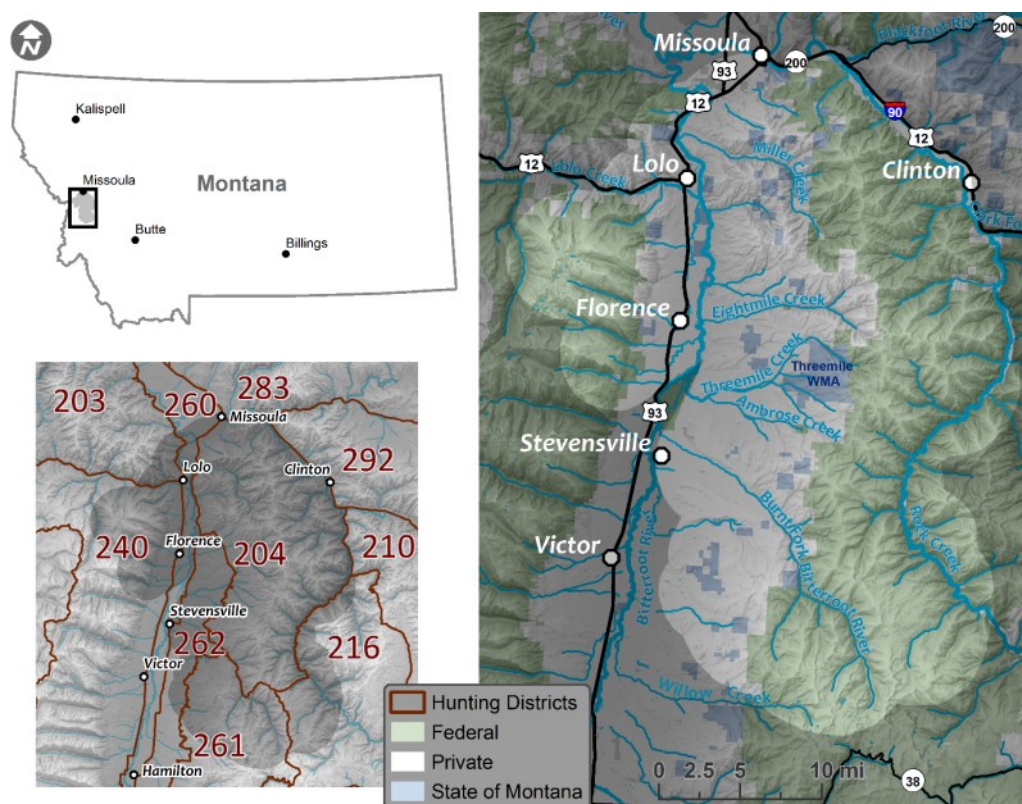
portant summer range for the elk population. However, limited information exists about the different migration strategies being used in this population, how much of the population currently migrates, and potential consequences of varying migration strategies to elk reproduction and survival. World-wide, loss of migration is a growing trend that can threaten resiliency of populations and ecosystems (Bolger et al. 2008, Harris et al. 2009). It is unknown if or to what extent the North Sapphire elk may have become less migratory, but unequal reproductive and survival rates of different migratory strategies or loss of traditional migratory strategies can be a concern for both hunters seeking harvest opportunities on public lands and private landowners experiencing increasing property damage.

Landowners and sportsmen approached MFWP with concerns regarding problematic distributions of elk in the northern Sapphire Mountains and current elk management strategies. In response, MFWP worked with collaborators to develop the North Sapphire Elk Research Project. The goals of this project were to collect information on public perceptions of elk status and management in the northern Sapphire Mountains, and to collect biological and movement information about the North Sapphire elk population. Specifically, project objectives were to:

- 1) Evaluate landowner and sportsman perceptions of elk management, including population management objectives, current elk hunting regulations, and issues related to elk hunting access,
- 2) Assess the health of the elk population by evaluating adult female body condition, pregnancy rate, and disease exposure rates,
- 3) Evaluate elk habitat and the distribution, availability, and quality of elk nutritional resources,
- 4) Estimate adult female and male elk survival rates and cause-specific mortality rates,
- 5) Evaluate female and male elk seasonal distributions, movement patterns, and migration strategies, and
- 6) Evaluate the effect of hunting on elk habitat selection and trade-offs of nutritional resources and harvest risk.



## Section 2 — North Sapphire Study Area



**Figure 2.1.** Land ownership and hunting districts in and around the North Sapphire study area located in the lower Bitterroot River watershed of west-central Montana, USA.

The study area encompasses approximately 2,400 km<sup>2</sup> of the northern Bitterroot Valley and includes the northern Sapphire Mountains and a portion of the Bitterroot Mountains south of Missoula, Montana (Figure 2.1). The study area boundary extends north to Lolo Creek and the Clark Fork River near the Missoula city limits and south to the headwaters of the Burnt Fork of the Bitterroot River drainage. The core of the study area is located in hunting district (HD) 204, with portions in HD 240 (in the Mormon Ridge and Carlton Creek area), HD 260 (along the Bitterroot River), HD 261 (in the headwaters of the Burnt Fork Drainage), and HD 262 (east of the Bitterroot River from Eightmile Creek to Skalkaho Creek). Elevations range from approximately 1000 to 3000 m. Yearly temperatures range from approximately -5 °C to 25 °C (PRISM Climate Group 2016). Land ownership is a matrix of public lands (59%), publicly accessible corporate timber lands (3%), and privately-owned residential and agricultural lands (38%) that dominate the valley bottom. The majority of public land is administered by the Lolo and Bitterroot National Forests and includes portions of the Selway-Bitterroot and Welcome Creek Wilderness Areas. Smaller tracts of public land are state trust lands administered by the Montana Department of Natural Resources and Conservation and the Threemile Wildlife Management Area administered by Montana Fish, Wildlife & Parks (MFWP).



Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), and a small population of bighorn sheep (*Ovis canadensis*) are sympatric with elk in the study area. Carnivores include mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), gray wolf (*Canis lupus*), coyote (*C. latrans*), and American black bear (*Ursus americanus*). One established wolf pack inhabits the southern portion of the study area (Montana Fish, Wildlife and Parks 2014) and additional wolves occa-

sionally travel throughout the study area.

The study area includes a variety of vegetation communities, with lower-elevation riparian areas, agricultural lands, and grasslands giving way to shrub- and conifer-dominated ecosystems at higher elevations. Bluebunch wheatgrass (*Pseudoroegneria spicata*) and fescues (*Festuca campestris*, *F. idahoensis*) tend to dominate grasslands. Sage-steppe ecosystems are dominated by big sagebrush (*Artemisia tridentata*), antelope bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus nauseosa*). Ninebark (*Physocarpus malvaceus*), chokecherry (*Prunus sp.*), serviceberry (*Amelanchier alnifolia*), mock-orange (*Philadelphus lewisii*), and snowberry (*Symphoricarpos albus*) comprise the dominant deciduous shrubs. Ponderosa pines (*Pinus ponderosa*) dominate lower elevation coniferous forests; forests at higher elevations are dominated by either lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), or a mix of Englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*).

Timber harvest and patchy fire history have resulted in habitats in varying successional stages. Timber harvests have declined approximately 69% and 76% on the Bitterroot and Lolo National Forests, respectively, from averages of 32.5 and 67.4 million board feet cut per year in the 1980s to 7.8 and 21.0 million board feet per year in the 2000s (U.S. Department of Agriculture, Forest Service 2016). Historically, this area of the Rocky Mountains experienced relatively frequent wildfires of low to medium severity during 1735–1900, with lower elevation Douglas fir-

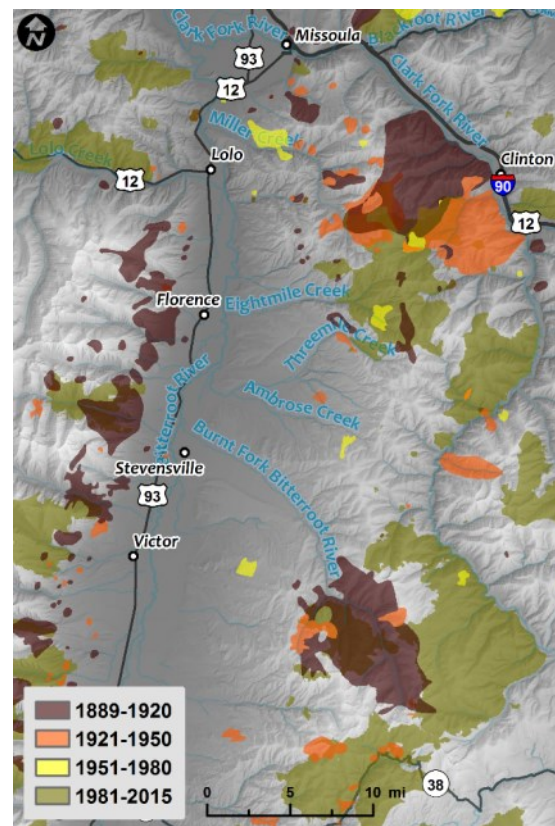


Figure 2.2. Fire history polygons from 1889–2015 in and around the North Sapphire study area located in the lower Bitterroot River watershed of west-central Montana, USA.



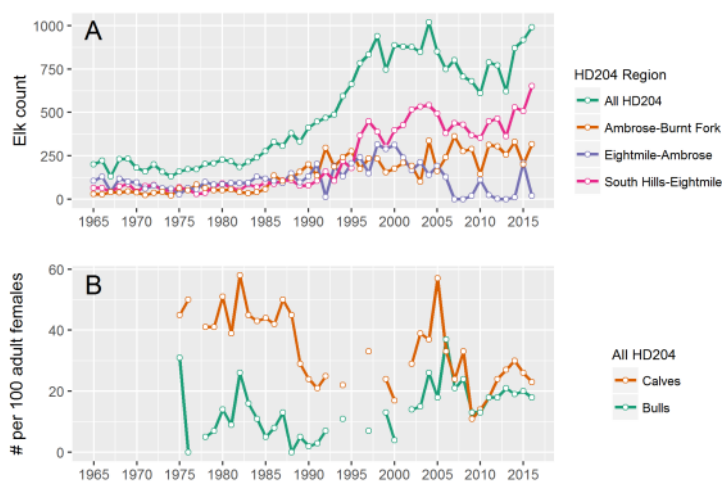
Ponderosa pine forests experiencing fire approximately every 10 years, and higher elevation subalpine fir and lodgepole pine forests experiencing fire approximately every 20–30 years (Arno 1976). However, in association with changes in forest management including active fire suppression in the early 1900s, wildfire activity decreased markedly in about 1920 (Arno 1976). Wildfire activity remained low through the 1990s. From the late 1990s until current time, fuel build-up from fire suppression policies resulted in more frequent, larger, and higher-severity fires throughout the region (Arno et al. 2000). These trends were mirrored within the study area (Figure 2.2), where wildfire activity is now common. More recently, large-scale wildfires occurred in 2000, 2003, and 2007, and smaller-scale fires occur annually. From 2000–2015, wildfires burned approximately 400 km<sup>2</sup> within the study area. Prescribed fires have also been applied intermittently on public lands throughout the northern Sapphire Mountains.

### Trends and recruitment

MFWP conduct aerial elk surveys on an annual basis each spring (late March–early April) from a fixed-wing airplane flying at low elevation. During surveys, elk are counted and classified into brow-tined bulls, spike bulls, unclassified bulls (primarily due to dropped antlers), adult females (including yearlings), and calves (9–10 months old). Surveys cover the entire range of the elk population within HD 204; however, sightability is not 100%. Elk counts therefore represent indices of elk population trends, and the number of calves per 100 adult females represents an index of calf recruitment. Within HD 204, counts are grouped into sub-regions, including the areas between the South Hills (Missoula) to Eightmile Creek, Eightmile Creek to Ambrose Creek, and Ambrose Creek to Burnt Fork, to evaluate spatial variability in elk population trends (Figure 2.3).

Elk counts in HD 204 increased from about 200–250 individuals during the 1960s–1980s to about 750 individuals since the early 2000s (Panel A, Figure 2.3; Edwards et al. 2015). More recent counts during 2014–2016 ranged from 870–990, with the second-highest count recorded since 1965 occurring in 2016. The South Hills-Eightmile region experienced the largest counts and greatest increase over time (Panel A, Figure 2.4).

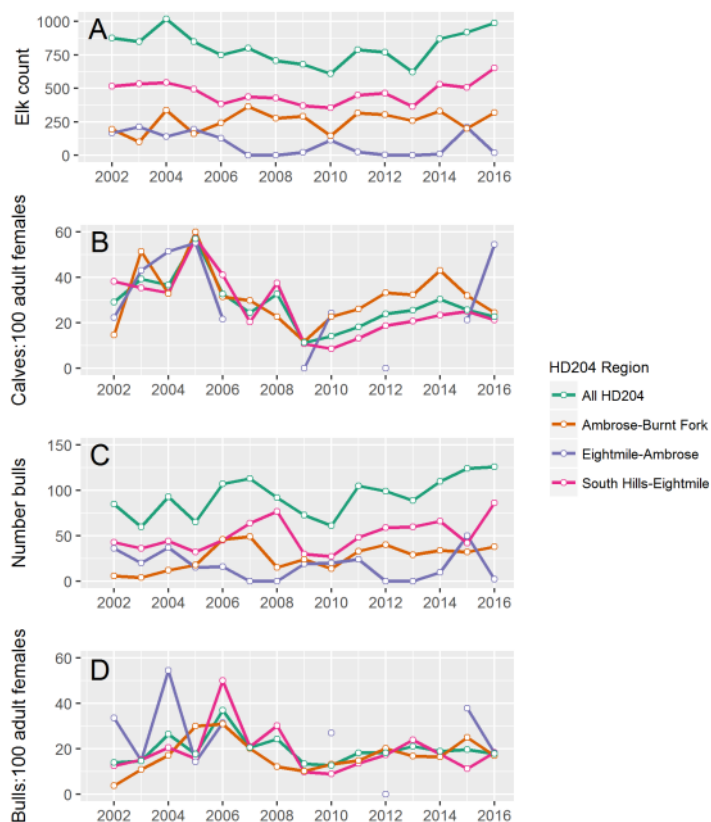
Recruitment ranged from 39–58 calves per 100 adult females during 1975–1988 in HD 204 (Panel B, Figure 2.3). During 1989–2002, recruitment approximately halved, ranging from 17–33. Recruitment then increased from 29 in 2002 to 57 in 2005, followed by a decline to 11 in 2009 (Panel B, Figure 2.4). From 2009, recruitment steadily increased to 30 in 2014 and decreased



**Figure 2.3. Annual elk counts (panel A) and number of calves and bulls per 100 adult female elk (panel B) in hunting district 204 from aerial spring surveys during 1965–2016.**

most recently to 22. These patterns were relatively consistent across regions within HD 204, except for the Eightmile-Ambrose region where data are lacking (Panel B, Figure 2.4).

The number of bulls per 100 adult female elk counted in HD 204 varied from 0–31 during 1975–2000 (Panel B, Figure 2.3). During 2002–2006, the number of bulls per 100 adult females increased from 14 to 37, followed by a decrease to 13 in 2009 and 2010 (Panel D, Figure 2.4; from 2002 onwards, the objective was set at 10 bulls per 100 adult females; see *Hunting regulations and harvest* below). During 2011–2016, the number of bulls per 100 adult females generally stabilized, ranging from 18–21. Between 2002 and 2010, the total number of bulls counted in HD 204 varied from 60–113 (Panel C, Figure 2.4). Due to higher proportions of unclassified elk in counts prior to 2008, the number of bulls may have been underestimated, and actual counts may be less variable. Since 2010, the number of bull elk has generally increased to 126 in 2016, the largest count recorded since at least 2002.



**Figure 2.4.** Annual elk counts (panel A), recruitment (calves per 100 adult female elk; panel B), number of bull elk counted (panel C), and bulls per 100 adult female elk (panel D) observed in hunting district 204 during aerial spring surveys in 2002–2016.

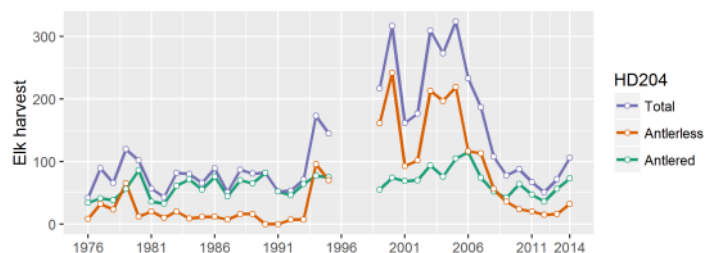
### Hunting regulations and harvest

Elk hunting regulations and harvest management are guided by the State of Montana Elk Management Plan (Montana Fish, Wildlife & Parks 2004). The management plan defines hunting regulations designed to increase or decrease elk populations toward population objective levels. In HD 204, elk population objectives were based on goals to minimize elk-related property and crop damage due to high elk densities and to provide adequate harvest opportunity. Elk population objectives in HD 204 changed during this study, but in 2015 the population objective was 600 (range of 480–720) observed elk for HD 204, with at least 10 bulls per 100 adult females and between 20–30 calves per 100 adult females. The elk management plan for this area also recommends maintaining an annual bull harvest of at least 40% brow-tined bulls, of which no less than 10% have 6 points on at least one antler.

Since at least 2003, MFWP had instituted a brow-tined bull or antlerless elk for youth-only regulation. This hunting regulation was maintained through 2016 with various additional

modifications to the antlerless harvest regulation made throughout the period to reduce or maintain the population within management objectives. The brow-tined bull or antlerless elk regulation was applied in the general season for the last week in 2004, the last two weeks in 2005, and the last three weeks in 2006–2009. The number of antlerless elk licenses declined, tracking decreasing elk counts, with 250 licenses in 2003–2004, 200 in 2005–2006, and 125 in 2007. Beginning in 2008, the number of elk counted in annual surveys was within management objectives, and antlerless licenses were eliminated. Instead, the brow-tined bull or antlerless opportunity for the last three weeks of general season was closed when the Darby hunter check station in the southern Bitterroot valley reached a quota of 200 (in 2008) or 100 (in 2009). In 2010 and 2011, 5 antlerless licenses were introduced. As elk populations began increasing and exceeding objectives, the number of antlerless licenses was increased to 30 in 2012–2014 and 100 in 2015–2016. From 2014 to 2016, elk counts in HD 204 have exceeded population objectives. Since at least 2002, the number of bulls per 100 adult females has exceeded the objective, averaging 19.6 (range 12.7–36.9).

Total elk harvested in HD 204 ranged from an estimated 42–120 elk during the late 1970s–1993, increased to 145–324 during 1994–2007, and decreased to 51–108 elk during 2008–2014 (Figure 2.5). Generally, from 1976–1995, antlered elk comprised the majority of the harvest totals. From 1999–2008, this pattern reversed, with antlerless making up most of the harvest, and from 2009–2016, the pattern reversed again. From 1976–2016, antlerless harvest has been variable, ranging from 0–242 yearly, and antlered harvest has ranged 33–115. From 2004–2014, with the exception of 2013, bulls with less than 6 points comprised the majority of the harvest, ranging from 22–87 (Figure 2.6). Since at least 2004 (no prior data available), harvest of brow-tined bulls with 6 points on at least one antler ranged from 10–41 and comprised more than 10% of the total harvest, satisfying the Elk Management Plan objectives.

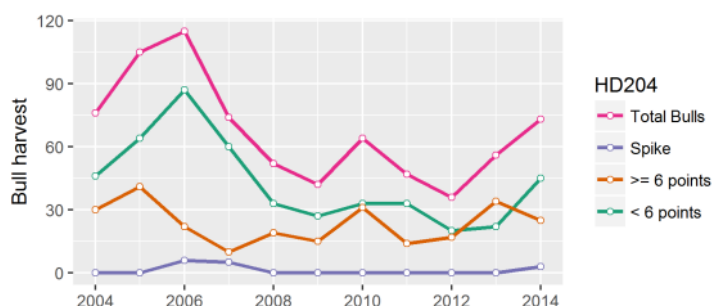


**Figure 2.5. Annual estimated total, antlerless and antlered elk harvested in hunting district 204 during 1976–2014.**

## Historic Movements in the Sapphire Mountains

### Sapphire Range Elk Ecology Study: 1970–1974

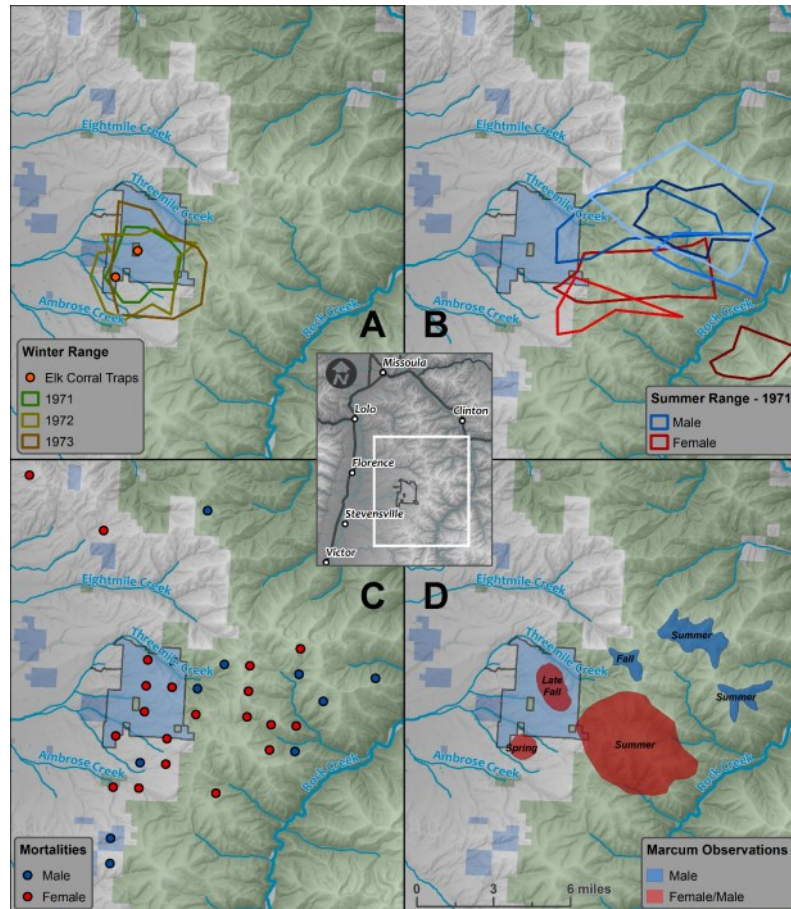
During 1970 to 1974, MFWP and the University of Montana (UM) conducted a study to better understand elk movements, distribution, habitat use, and harvest rates of the elk population occupying the Bitterroot-Rock Creek Divide and wintering on



**Figure 2.6. The total estimated number of male elk harvested and antler characteristics of harvested male elk in hunting district 204 during 2004–2014.**

the Threemile Wildlife Management Area (Figure 2.7; Ream et al. 1971, 1972). This project was initiated as part of the Montana Cooperative Elk-Logging Study in response to concerns that logging practices were affecting elk distributions and movements. Results of this project were presented as part of Ph.D. dissertations (Beall 1974, Marcum 1975). During winters 1970–1974, elk were baited by hay and trapped in two wooden corral traps located on the Threemile Wildlife Management Area (Panel A, Figure 2.7). Elk received an aluminum ear-tag and were fitted with either a VHF radio-collar or a colored marking collar. Elk were aged by tooth replacement and wear, or, if older than 1.5 years, an outermost incisor was pulled for aging by tooth sectioning (Ream et al. 1971). VHF-collared elk were relocated aerially and by ground through the duration of the study.

A total of 64 elk were captured: 16 calves (10 female, 6 male), 12 yearlings (5 females, 7 spikes), 3 adult males, and 33 adult females. The average age in years of female and male elk at capture was 3.0 (range 0.5 to  $\geq 10.5$ ) and 1.5 (range 0.5 to 6.5), respectively. Twenty-nine elk were outfitted with radio-collars and ear-tags, and 33 elk were marked with either ear tags or visibility collars. Radio-collar relocation data and maps were limited in the available reference literature (Figure 2.7; Ream et al. 1971, 1972, Beall 1974, Marcum 1975), but ear tag and collar returns were recorded on recovered capture and mortality datasheets that were coalesced for the current project. Winter range of VHF-collared individuals was similar each year from 1971–1973 (Panel A, Figure 2.7). Summer ranges were reported for a limited number of VHF-collared individuals ( $n = 7$ ) from June–October 1971 but were roughly distinct in location for male and female elk (Panel B, Figure 2.7; Ream et al. 1972).



**Figure 2.7.** Elk location data from the Sapphire Range Elk Ecology Study 1970–1974 focused around the Threemile Wildlife Management Area (blue polygon). Panel A: Corral trap locations used to capture elk and annual winter ranges of VHF-collared male and female elk for 1971 (5 individuals), 1972 (8 individuals), and 1973 (6 individuals). Panel B: Summer ranges of 7 VHF-collared elk monitored during June–October 1971 (colors indicate boundaries for each individual elk as delineated by the smallest polygon enclosing all relocations of each elk). Panel C: Mortality locations (1971–1982) of ear- & collar-marked elk (showing only known locations and excluding HD130 and HD298 mortalities). Panel D: Areas of significant seasonal use by elk from the late 1970’s to the early 1980’s as identified by Les Marcum in the fall of 2014.



Male elk summer ranges (17–52 km<sup>2</sup>) generally encompassed the upper reaches of Welcome and Threemile Creeks, while female elk summer ranges (10–27 km<sup>2</sup>) generally encompassed the upper reaches of Cinnabar and Wheelbarrow Creeks. In fall 2014, Dr. Les Marcum was interviewed to provide information on areas of significant seasonal use by male and female elk from the late 1970s to early 1980s (Panel D, Figure 2.7). Marcum reported male and female elk spring range occurred between Wheelbarrow and Grayhorse Creeks. Male summer ranges primarily at upper elevations north of Welcome Creek; female (and some male) elk summer ranges included a broader area along the upper reaches of Cinnabar and Cinnamon Bear Creeks. Late-fall range for male and female elk was within the Threemile Wildlife Management Area.

Mortality events and locations were reported for 42 of the 64 marked elk from 1971–1982 (Panel C, Figure 2.7). Thirty-nine (28 females and 11 males) of the 42 mortalities occurred in HD 204. The remaining mortalities occurred in other hunting districts: 1 male elk in HD 130 (on the Flathead Indian Reservation in the southern Mission Mountains) in January 1981, 1 female elk in HD 298 (Ovando-Helmville area north of Drummond) in November 1981, and 1 male elk in HD 216 (north of West Rock Creek) in September 1974. Twenty-six of the 42 elk mortalities were due to hunter harvest, 2 died of unknown causes outside of the hunting seasons, 1 died from injuries sustained during capture, and 13 died of unknown causes coinciding with the timing of the fall hunting season.

According to notes in the trapping files, the oldest and largest male elk marked was a 9.5-year-old captured at 6.5 years old in 1971 and harvested as a 6x10 in the Welcome Creek Wilderness in 1974. Other older male elk included: an 8.5-year-old captured as a spike in 1974 and harvested (no size recorded) on the Flathead Indian Reservation (mentioned previously) in 1981; a 5.5-year-old captured as a calf in 1971 and harvested (no size recorded) in HD 204 in 1976; and a 4.5-year-old captured as a calf in 1972 and harvested as a 6x6 in HD 204 in 1976. The oldest female elk marked were 13.5 years old, and included an elk captured at 3.5 years old in 1972 and harvested in Ambrose Creek in 1982 and an elk captured at 10.5 years old in 1970 and harvested on Greyhorse Point in 1973.

#### Summer-Fall Habitat Selection (Les Marcum Ph.D. Dissertation): 1971-1973

In association with the Sapphire Range Elk Ecology Study above, Les Marcum (graduate student at University of Montana) evaluated summer-fall (June-November) elk movements and habitat selection related to roads and timber harvest based on location data from 20 VHF-collared elk (15 female, 5 male) during 1971 to 1973. The study area included the Threemile Wildlife Management Area and the region to the west in the Welcome Creek Wilderness Area and bordered by Rock Creek (see Figure 2.7).

Marcum found higher than expected use of *Pseudotsuga menziesii*/*Calamagrostis rubescens* and *Abies lasiocarpa*/*Galium triflorum* habitat types, canopy covers of 26 to 75%, south and southwest aspects, gentle (0–15°) slopes, and mid-elevations (5,350 to 6,349 feet). Drainage bottoms near water were also intensively selected for by elk. However, between-year differences in selection occurred, highlighting the variability of selection in response to differing weather scenarios. Elk selected drier plant communities in 1972, a year with higher than normal

spring precipitation and a cool and moist summer, but more mesic plant communities in 1971 and 1973, relatively warm and dry years. During the fall hunting seasons, elk increased use of high (> 75%) canopy cover forests. Female elk used *Pseudotsuga menziesii*, *Pinus ponderosa*, and *Abies lasiocarpa* habitat types more than male elk, excepting forests associated with *Xerophyllum tenax* and the *Abies lasiocarpa/Vaccinium scoparium* habitat type. During the calving period in June, female elk used plant communities at lower elevations adjacent to areas of heavy canopy cover and nearer to water than male elk. Male elk used warmer exposures throughout the summer-fall, whereas female elk used cooler exposures from July through September. Male elk also generally used steeper slopes, higher canopy cover, and higher elevations than female elk.

Marcum found roads and logging activities to be an important element of elk selection. Elk selected against roads open to motorized use, against areas within 550 yards of roads open to motorized use, for areas greater than 1 mile from roads open to motorized use, and for roads closed to motorized use, particularly during the hunting season. This pattern of selection was stronger for male elk than female elk. Elk selected for partially-logged areas and against clearcut areas, with female elk more often using areas near to either logging type as compared to male elk. While partially-logged areas were more acceptable to elk, Marcum suggests that because the majority of the forests in the study area had undergone multiple logging events, the preference may indicate a lack of choice for the elk and that there may not be strong evidence that logging activities benefit elk.



## Section 3 — Landowner and Hunter Survey

### Background

The North Sapphire elk population in HD 204 is located in Missoula's backyard, and as such provides important hunting and recreational opportunities. Landowners and sportspersons from this area approached MFWP with concerns regarding problematic elk distributions, current elk numbers, how hunting should be managed, and hunting access. In response, MFWP conducted 2 surveys to gather baseline information from both resident elk hunters and private landowners regarding the following:



1. *Current elk population management objectives*
2. *Current elk hunting regulations*
3. *Specific issues related to elk hunting access*

The first survey, the resident elk hunter survey, was sent to a randomly selected sample of resident elk license holders who live in Missoula, Ravalli, and Granite counties in Montana. The second survey, the private landowner survey, was sent to all private landowners that owned > 160 acres in HD 204. The purpose of the surveys was to identify and compare the perceptions of resident hunters and landowners regarding elk populations and harvest management in HD 204.

### Results

#### Participation in the resident elk hunter survey

In mid-June 2014, surveys were sent to a randomly selected sample of N = 5,000 resident elk license holders who live in Missoula, Ravalli, and Granite counties in Montana. These counties were selected for study sampling based on information from FWP's Hunter Harvest Survey that revealed 92 percent the elk hunters who reported that HD 204 was one of their top three districts to hunt elk in 2012 reside in the geographic area comprising these three counties. In total, surveys were successfully delivered to 4,442 of the 5,000 resident elk hunters randomly selected for study. A replacement survey was sent to all survey non-respondents approximately three weeks following the initial mailing of the survey. There were a total of 1,829 respondents, which resulted in an overall 41% survey response rate. Thirty percent of the survey respondents reported hunting elk in HD 204 at some point in time during the past ten years. These resident elk hunters were the focus of the resident elk hunter survey.

Characteristics of the hunter survey respondents included:

- Sixty percent of the respondents reported elk hunting in HD 204 is important or very important to them. Fourteen percent reported elk hunting in this district is unimportant or very unimportant to them.
- The most frequently mentioned motivations reported by respondents for hunting elk in the HD 204 area included: *It's close to home, to obtain meat/food, for recreational purposes, and hunting heritage/familiarity with the area.*
- Twenty percent of respondents reported they primarily hunt elk in HD 204 during the archery elk season; 63% reported hunting primarily during the general rifle season; and, 17% reported hunting an equal amount of time during the archery and general rifle seasons. On average, respondents reported hunting elk about nine days per year in HD 204.
- The average age of respondents was 48 years. Ninety-two percent of the respondents were male; 8% were female.

#### Participation in the private landowner survey

During the same timeframe as the resident elk hunter survey, surveys were also sent out to all (N = 78) private landowners identified in Montana's State Cadastral database as owning at least 160 acres in the geographic vicinity of Hunting District 204. In total, surveys were successfully delivered to 71 of these landowners. A replacement survey was sent out to all survey non-respondents approximately three weeks following the initial mailing of the survey. There were a total of 33 respondents, which resulted in an overall 47 percent survey response rate.

Characteristics of the landowner survey respondents included:

- Nearly 70% of respondents reported their primary motivation (or reason) for owning property in the HD 204 area was for wildlife-related reasons (e.g., viewing, wildlife habitat, conservation), recreation, land conservation, and/or preserving open space. Thirty percent of the respondents reported agriculture or livestock production as the primary motivation for owning land in the area.
- Forty-nine percent of the respondents reported owning 160–319 acres; 24 percent reported owning 320–1,279 acres; 15% reported owning 1,280–2,559 acres; and, 12% reported owning 2,560 or more acres in the HD 204 area. On average, respondents reported owning their property in the HD 204 area for 27 years.
- The average age of respondents was 60 years. Seventy-nine percent of the respondents were male; 21% were female.

#### Perceptions of elk numbers

Hunters and landowners were asked their perceptions of current elk numbers in HD 204 during the hunting season. In general, both groups were in agreement that elk numbers appear lower than desirable (Figure 3.1 & 3.2). For instance, on a scale from 1 (too few) to 5 (too many), nearly 70% of the resident hunters scored overall numbers of elk in HD 204 during the hunting season as being a "1" or a "2". This compares to 66% of private landowners who rated overall elk numbers on their land during the hunting season as being a "1" or "2".

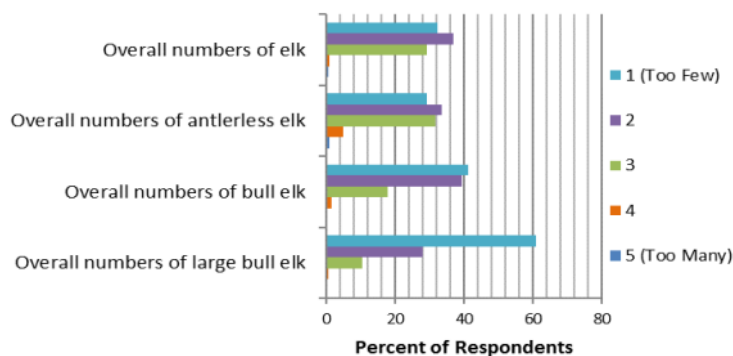
Hunters and landowners were also asked about their perceptions of changes in elk numbers over time. Once again, both groups were in relative agreement that there appear to be fewer elk now compared to the past. It is worth noting that a much higher percentage of hunters reported they believe there are currently fewer elk. For instance, 73% of the resident hunters reported they are currently seeing fewer overall numbers of elk in HD 204 during the hunting season compared to the past. This compares to 46% of private landowners who reported they are currently seeing fewer elk on their property during the hunting season as compared to the past.

Both private landowners and resident elk hunters reported similar reasons for why they believe elk numbers appear to be decreasing. The most frequently mentioned reasons reported by respondents were as follows (listed in decreasing order of magnitude received):

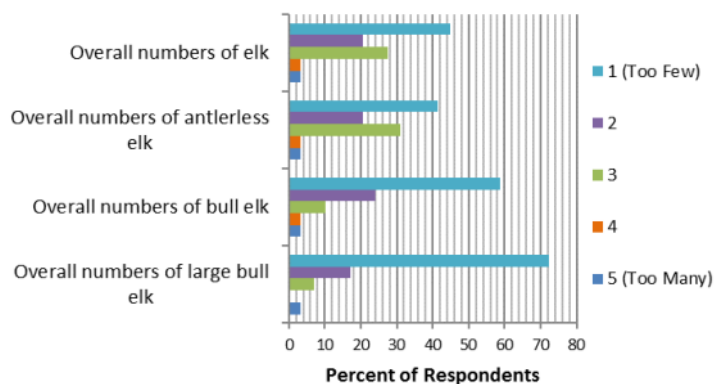
- Wolves
- Too much hunting pressure; the area is over hunted
- Concerns about predators in general (e.g., wolves, bears, mountain lions, etc.)
- Weather/climate change

#### Perceptions of elk hunting regulations and overall elk management

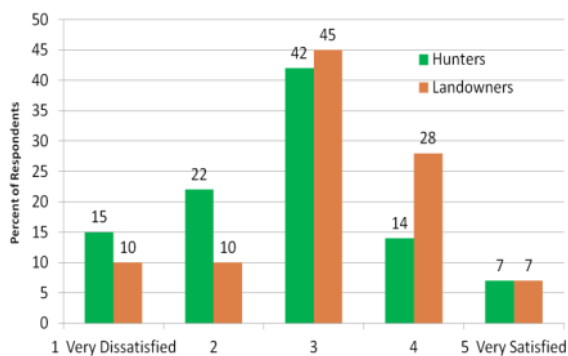
In total, 63% of respondents to the resident elk hunter survey and 80% of respondents to the private landowner survey reported general satisfaction with the current elk hunting regulations in HD 204 (Figure 3.3). At the time of the survey, current regulations were as follows: *Brow-tined bull or antlerless elk during the archery only season. Brow-tined bull during the general rifle season (plus antlerless elk for youths only ages 12–15). Additionally, there are 30 antlerless elk B licenses available by drawing for this hunting district.*



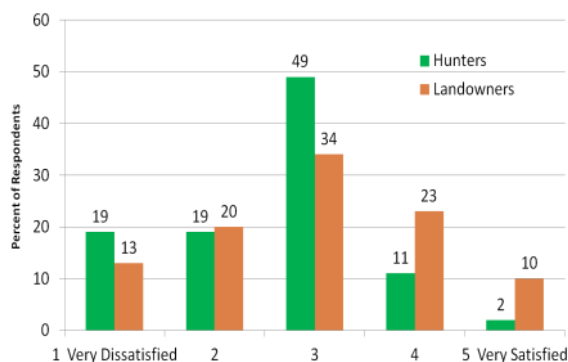
**Figure 3.1. Resident elk hunter response to: “At present (e.g., during the past three years), on a scale from 1 (too few) to 5 (too many), how would you rate the following in HD 204 during the hunting season?”**



**Figure 3.2. Private landowner response to: “At present, on a scale from 1 (too few) to 5 (too many), how would you rate the following ON YOUR PROPERTY during the hunting season**



**Figure 3.3. Resident elk hunter and private landowner response to: “On a scale from 1 (very dissatisfied) to 5 (very satisfied), how satisfied are you with the current elk hunting regulations in HD 204?”**



**Figure 3.4. Resident elk hunter and private landowner response to: “On a scale from 1 (very dissatisfied) to 5 (very satisfied), how satisfied are you with the current elk management in HD 204?”**

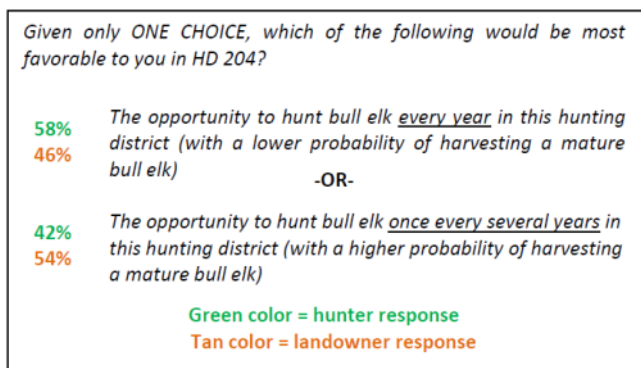
About 62% of the respondents to the elk hunter survey and 67% of the respondents to the landowner survey reported general satisfaction with current elk management HD 204 (Figure 3.4).

Respondents to both the elk hunter and landowner surveys provided numerous comments regarding current elk hunting regulations and elk management in general. The most frequently received comments were (listed in decreasing order of magnitude received):

- *Concern about wolves and their effect on the elk population in the area*
- *Concern about predators in general*
- *Concerns about “harboring” and that elk are located primarily on privately owned land that offers little or no hunting access*
- *Concerns about declining elk numbers*

### Preferences for elk hunting regulations

Managing for higher numbers of mature bull elk (e.g., bulls 4–5 years of age or older) may require implementing more restrictive hunting regulations. With this in mind, both elk hunters and landowners were asked the following forced-choice question to help assess how restrictive elk hunting regulations should be in HD 204.



### Elk hunting access

Two-thirds of respondents to the landowner survey reported they allow elk hunting on at least a portion of the property they own in the HD 204 area. Thirty percent of those landowners reported they do not allow cow elk hunting. Ten percent of those landowners reported they do not allow bull elk hunting.

Of those landowners who allow cow elk hunting, 69% reported they primarily manage antlerless elk hunting using a non-Block Management system (without fees) that involves mostly hunters who are family or friends. Of those landowners who allow bull elk hunting, 81% reported they primarily manage bull elk hunting using a non-Block Management system (without fees) that involves mostly hunters who are family or friends. None of the landowners who allow elk hunting reported they outfit, lease hunting opportunities, or charge hunters access fees to hunt elk on their property.

With respect to the hunter survey, 85% of the respondents reported they primarily hunt on public land in HD 204. Only 2% reported primarily hunting on non-Block Management private land (without a fee) that is not owned by their family, relatives, a close friend, or friends of family/relative.

### **Discussion**

Survey results suggest that hunters and landowners agree on several points. There appears to be general hunter and landowner satisfaction with elk management in HD 204, despite the perceptions of both groups that elk numbers appear lower than desired. The biggest concerns expressed by survey respondents revolved around topics such as wolves (and predators in general), excessive hunting pressure on elk, and a perception that elk are typically found on privately owned lands with little or no hunting access during the hunting season.

Hunters and landowners were in less agreement with one another regarding their preferences for elk hunting regulations in HD 204. Nearly 60% of the resident elk hunter survey respondents prefer less restrictive elk hunting regulations that do not limit bull hunting opportunity; however, > 50% of respondents to the private landowner survey preferred more restrictive elk hunting regulations that allowed the opportunity to hunt only every couple of years with goals of increasing the chances of harvesting a mature bull elk. The response of resident elk hunter survey respondents were similar to those reported from a statewide mule deer hunter preference survey, where 55% of resident hunters favored non-restrictive mule deer buck hunting regulations that do not limit buck hunting opportunity (Lewis et al. 2011).

Survey results also demonstrate that gaining access to hunt elk on privately owned land in HD 204 may be challenging if hunters do not have a direct connection to a landowner. These results reflected a general pattern evidenced across Montana based on another survey of statewide resident deer, elk, antelope, and upland game bird hunters that suggested that securing access to hunt on non-Block Management privately owned land was becoming challenging for those hunters who do not have a direct connection with a landowner (Lewis et al. 2014).

## Section 4 — Elk Body Condition, Pregnancy, and Disease Exposure

### Background

The nutritional condition of adult female elk can have important consequences to elk populations through altered survival and reproductive performance (Cook et al. 2004, 2013, 2016). Poor nutritional condition can decrease overwinter survival, shift timing of birth, reduce calf weight at birth, reduce juvenile survival, and reduce pregnancy rates (Gaillard et al. 2000, Cook et al. 2004, 2013). Nutritional resources acquired during summer are of particular importance to ungulate reproduction and survival (Monteith et al. 2013, Cook et al. 2013). During summer, female ungulates require sufficient high quality forage to compensate for lower forage quantity and quality during winter, recover the energetic costs of lactation, and build body reserves to survive and maintain pregnancy during the winter (Cook et al. 2004). Elk in higher nutritional condition, as indicated by percentage ingesta-free body fat, have higher rates of pregnancy than those in lower nutritional condition (Cook et al. 2004, 2013). Additionally, density-dependent reductions in per-capita nutritional resources have the potential to reduce body condition and, consequently, pregnancy rates (Stewart et al. 2005). Our goal was to assess and summarize winter elk body condition and pregnancy rate of the North Sapphire elk population to characterize the overall nutritional status of the population.

Diseases such as brucellosis or chronic wasting disease may also be important drivers of wildlife population demography through suppression of survival and reproductive rates. Additionally, disease in wildlife populations may have important impacts to landowner tolerance for wildlife. Our goal was to estimate levels of disease exposure in the North Sapphire elk herd to assess the overall population health.

### Methods

We captured adult (> 1.5 years old) elk in February 2014 by helicopter net-gunning and darting in accordance with approved animal welfare protocol (IACUC #FWP19-2013). We estimated elk age by tooth eruption and wear patterns. We measured chest girth and assessed body condition using a portable ultrasound machine to estimate body mass and levels of ingesta-free body fat (IFBF) following the revised methods of Cook et al. (2010) that included an allometrically scaled MAXFAT index. We could not reliably determine if elk had lactated the previous summer and fall. We collected a blood sample and screened blood serum for exposure to a suite of common diseases previously known to occur in Montana. These diseases include brucellosis (*Brucella abortus*), para-influenza 3, infectious bovine rhi-



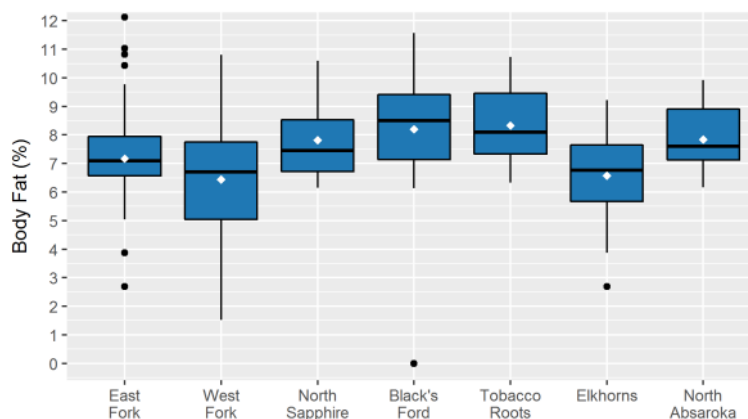


notracheitis, bovine respiratory syncytial virus, bovine viral diarrhea, and leptospirosis (*Leptospira*). We also determined pregnancy status from presence of pregnancy-specific protein-B in the blood serum (Noyes et al. 1997).

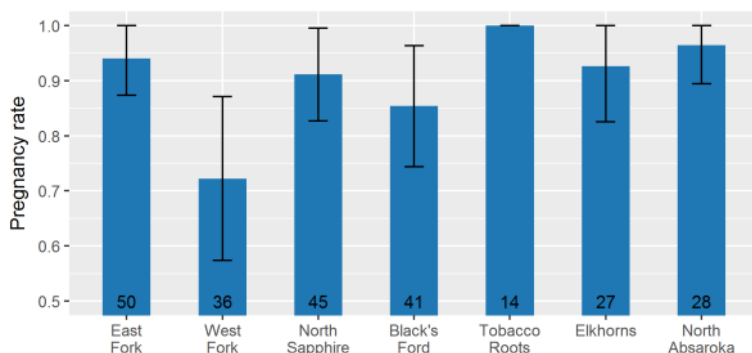
## Results

### Elk body fat

We captured and sampled 45 adult female elk during February 2014. Estimated age averaged 6.3 years (95% confidence interval [CI] = 5.7–6.9, range = 3–10,  $n = 45$ ). IFBF averaged 7.8% (95% CI = 7.4–8.2%, range = 6.1–13.3%,  $n = 44$ ). IFBF levels for the North Sapphire population were similar to the majority of southwestern Montana populations sampled 2013–2015 (Figure 4.1). Compared to the Black's Ford and Tobacco Roots populations captured during the same year (2014), IFBF levels for the North Sapphire population averaged 0.4 and 0.5% lower, respectively, but were not significantly different based on overlapping confidence intervals (7.6–8.7 and 7.6–9.0%, respectively). IFBF levels were significantly higher than the Elkhorn population sampled in 2015 ( $\bar{x} = 6.6\%$ , 95% CI = 5.9–7.2%).



**Figure 4.1.** Estimates of percent winter ingesta-free body fat (IFBF) for female elk in populations across southwestern Montana sampled during 2011–2015. Dark horizontal bars and white diamonds represent median and mean IFBF, respectively. Sampling in the East Fork and West Fork occurred 2011–2013, North Sapphire, Black's Ford, and Tobacco Roots occurred 2014, and Elkhorns and North Absaroka occurred 2015.



**Figure 4.2.** Estimates of mean pregnancy rate for female elk in populations across southwestern Montana during winter 2011–2015. Whisker lines represent 95% confidence intervals. Numbers at bottom are respective sample sizes. Sampling in the East Fork and West Fork occurred 2011–2013, North Sapphire, Black's Ford, and Tobacco Roots occurred 2014, and Elkhorns and North Absaroka occurred 2015.

### Pregnancy rate

Average pregnancy rate was 0.91 (95% CI = 0.83–1.0,  $n = 45$ ), similar to the average rate of 0.89 across southwestern Montana populations sampled 2011–2015 (Figure 4.2). In the North Sapphire population, IFBF levels for non-pregnant elk averaged 7.1% (95% CI = 6.5–7.8%,  $n = 4$ ) and for pregnant elk averaged 7.9% (95% CI = 7.4–8.3%,  $n = 40$ ; Figure 4.3). Average IFBF levels in sampled southwestern Montana populations were 6.2% for non-pregnant

elk (varying from 3.3–7.3%) and 7.9% for pregnant elk (varying from 6.8–8.5%). Small sample sizes for non-pregnant elk make comparisons across populations difficult.

## Disease exposure

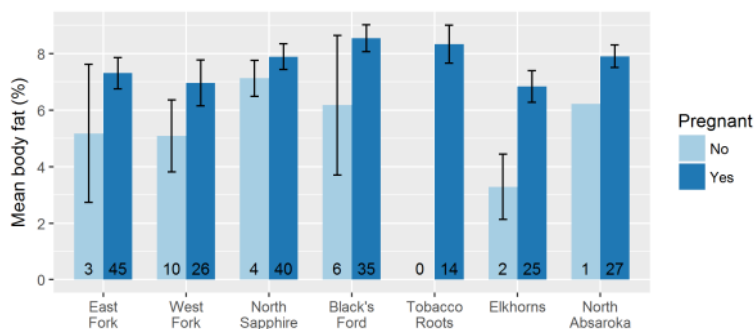
Serologic evidence for *Brucella abortus* exposure was not detected in any of the North Sapphire elk sampled (n = 45, Table 4.1). Levels of exposure to other diseases were similar to levels observed in other southwestern Montana elk populations.

## Discussion

Our assessment of the nutritional status and overall health of the North Sapphire elk population based on IFBF estimates, pregnancy rates, and disease exposure testing suggest that the population is in overall good health and condition. Winter body-fat levels of adult female elk were similar to elk in other parts of southwestern Montana and pregnancy rates were normal with no evidence of nutritional or disease-related limitations. Winter body fat and pregnancy rate were higher than populations in other regions of western U.S. (Cook et al. 2013). This information suggests that the summer nutritional resources of the North Sapphire population is of adequate quality and not limiting this population (Monteith et al. 2013, Cook et al. 2013, Proffitt et al. 2016a). Additionally, we found no evidence that elk were exposed to brucellosis or other diseases that affect reproduction or survival.

**Table 4.1. Annual exposure levels to *Brucella abortus* (Brucella), *Leptospira* spp. (Lepto), para-influenza 3 (PI3), infectious bovine rhinotracheitis (IBR), bovine viral diarrhea (BVD) and epizootic hemorrhagic disease (EHD) from serological screening of adult female elk in Bitterroot Valley populations sampled during 2013 – 2014.**

Population	Year		Brucella	Lepto	PI3	IBR	BVD	EHD
North Sapphire	2014	Sample Size	45	45	45	45	45	45
		# Exposed	0	1	7	7	0	0
		% Exposed	0	2.2	15.5	15.5	0	0
W Fork Bitterroot	2013	Sample Size	22	22	22	22	22	-
		# Exposed	0	0	5	2	0	-
		% Exposed	0	0	22.7	9.1	0	-
E Fork Bitterroot	2013	Sample Size	20	20	20	20	20	-
		# Exposed	0	0	5	4	2	-
		% Exposed	0	0	25.0	20.0	10.0	-



**Figure 4.3. Estimates of mean percent ingesta-free body fat (IFBF) for pregnant and non-pregnant adult female elk in populations across southwestern Montana during winter 2011–2015. Whisker lines represent 95% confidence intervals. Numbers at bottom are respective sample sizes. Sampling in the East Fork and West Fork occurred 2011–2013, North Sapphire, Black's Fork, and Tobacco Roots occurred 2014, and Elkhorns and North Absaroka occurred 2015.**

## Section 5 — Elk Nutritional Resources & Effects of Wildfire

### Introduction

Forest management practices, including grazing, prescribed fire, wildfire exclusion, and timber management, modify ecological processes, manipulate vegetation (Keane et al. 2002, Wondzell and King 2003, Fisher and Wilkinson 2005, Noss et al. 2006, Long et al. 2008, Hebblewhite et al. 2009, Allred et al. 2011, Cook et al. 2016), and have the potential to affect the availability and distribution of nutritional resources available for wildlife populations. Multiple studies have confirmed the importance of nutritional resources on ungulate reproduction and survival (Monteith et al. 2013, Cook et al. 2013, 2016, Proffitt et al. 2016a). Nutritional resources available on summer ranges are important because female ungulates must meet the nutritional demands of lactation and accrue adequate fat reserves for establishing pregnancy and surviving the winter. Additionally, the distribution of nutritional resources is a primary driver of ungulate distributions (Bailey et al. 1996, Wilmshurst et al. 1999, Sawyer and Kauffman 2011, Ranglack et al. 2016). There is a need to better understand the effects of forest management and forest disturbances on ungulate nutritional resources to guide management actions that benefit ungulate populations.

Fire presents an important yet complex consideration in ungulate habitat management. Fire affects wildlife nutritional resources by altering the composition, abundance, and quality of forage plants (Keay and Peek 1980, Fisher and Wilkinson 2005, Sachro et al. 2005, Van Dyke and Darragh 2007, Long et al. 2008, Lord and Kielland 2015, Sittler et al. 2015, Romme et al. 2016). The area burned by wildfire annually in the United States has increased since 1995 (Stephens and Ruth 2005, Dennison et al. 2014), and is projected to further increase due to fuel load accumulation associat-



ed with historic fire suppression (Keane et al. 2002, Ryan et al. 2013) and global climate change (Dale et al. 2001, Brown et al. 2004). In addition to wildfire, prescribed fire is increasing as a method of reducing excessive fuel loads and restoring historic fire return intervals. However, whether prescribed fires adequately mimic natural conditions remains a matter of contention (Koyama et al. 2012, Ryan et al. 2013), and prescribed fires may have positive or negative effects on ungulate nutritional resources (Peck and Peek 1991, Long et al. 2008).

Our goals were to evaluate the effects of wildfire and prescribed fire on ungulate forage quality and abundance within the Bitterroot Valley of west-central Montana and, using data collected from within 3 elk population ranges, assess the wildfire-related variations in ungulate forage during the past century. A better understanding of the effects of fire on forage is needed to infer the nutritional and potential demographic consequences of fire on ungulate popula-

tions, and to better understand how forest fires and fire management practices may affect ungulate populations over time.

## Study area

The study area included the ranges of the North Sapphire population and 2 additional populations in the southern Bitterroot Valley: the East Fork and West Fork populations (Figure 5.1; Proffitt et al. (2016a, 2016b). This project built off of previous work conducted in the southern Bitterroot Valley (Proffitt et al. 2016a). We sampled vegetation in the North Sapphire range during 2014–2015 and in the East Fork and West Fork ranges during 2012–2015.

Wildfire activity has been common and is more recently the primary disturbance throughout the Bitterroot Valley. From 1889–1949, wildfires burned on average  $32 \text{ km}^2$  annually, decreasing to  $16 \text{ km}^2$  during 1950–1999. From 2000–2015, wildfire activity increased, with large-scale wildfires occurring in 2000, 2003, 2007, and 2011 and smaller-scale fires occurring annually. During this period, wildfires burned approximately  $2,043 \text{ km}^2$ , averaging  $159 \text{ km}^2$  annually. Prescribed fire has been applied intermittently on public lands throughout the Bitterroot Valley, beginning primarily in the early 1990's. During 1990–1999, prescribed fires burned on average  $39 \text{ km}^2$  annually, decreasing to  $17 \text{ km}^2$  during 2000–2015.

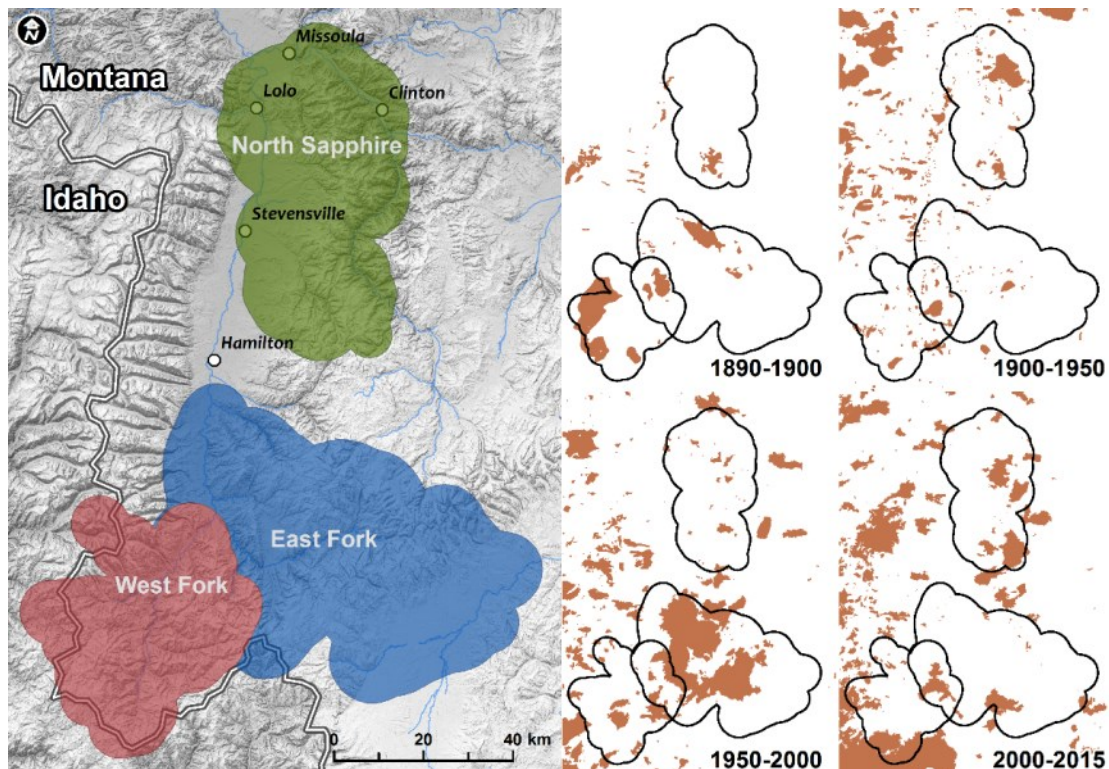


Figure 5.1. The North Sapphire, East Fork, and West Fork elk population annual ranges and the 1890–2015 wildfire patterns overlaid on the annual ranges. Orange-red polygons indicate fires occurring within the indicated time span.



## Methods

We used a combined ground and remote-sensing based approach to develop landscape-scale summer elk forage quality and abundance models for western Montana (e.g., (Hebblewhite et al. 2008, Proffitt et al. 2016a, 2016b). Our general approach (detailed below) was to first determine the dominant forage species in the North Sapphire, East Fork, and West Fork elk summer diets. We then sampled locations across a gradient of fire histories to evaluate spatial and temporal effects of wildfire and prescribed fire on forage abundance and quality. Finally, we used historic wildfire data to estimate the fire-related variability of forage within the 3 different elk population summer ranges during the past 115 years.

### Forage plant identification and plant sampling

We identified the important summer forage species in Bitterroot elk diets by collecting pellet samples from within each population range and using fecal plant fragment analysis to identify forage species. We ranked the top forage plant species for each elk population, selected the species that constituted 95% of the total diet, and combined the species from each elk population to represent the important summer forage species. We screened our plant data (described below) to include only these forage species in estimates of forage quality and abundance.



Within each population range, we estimated plant biomass and species composition at random plot locations within 12 vegetation cover types based on a proportional allocation sampling design (Krebs 1989). The 12 cover types included mesic forest systems with 3 wildfire histories (late-successional areas burned > 15 years prior, mid-successional areas burned 6–15 years prior, and early-successional areas burned 0–5 years prior); dry to mesic montane mixed conifer forests with 3 wildfire histories (late-successional, mid-successional, and early-successional); early-successional dry to mesic montane mixed conifer forests that were subject to a prescribed understory burn within 0–5 years (Long et al. 2008); open grasslands, shrublands, and woodlands; valley bottom riparian; montane riparian; irrigated agriculture; and dry agriculture. The prescribed understory burn sampling locations occurred only in dry to mesic montane mixed conifer forests that were not treated post-fire with weed spraying or forest thinning.

At each sampling site, we established a 40 m transect along the contour of the slope. We recorded species composition and percent cover of forbs, shrubs, and graminoids at five 1 m<sup>2</sup> quadrats every 10 m along each transect. At the 0 m, 20 m, and 40 m quadrat, we established a nested 0.25 m<sup>2</sup> clip plot and collected all graminoid and forb biomass > 1 cm above ground. On shrubs, we clipped all leaves and non-woody stems (however, see changes to sampling methods below).

Plant phenology affects plant nutritional availability, and needs to be accounted for in plot-based sampling of forage resources. To estimate variation in phenological stage of each forage species, we estimated the dominant phenological stage (emergent, flowering, fruiting, mature seed, or senescent) of each.

#### Forage quality and abundance

To estimate the quality (i.e., digestible energy per gram or kcal/g) of forage plant species, we collected samples of forage species during each major phenological stage and estimated dry matter digestibility using sequential detergent fiber analysis (Van Soest 1982; Wildlife Habitat and Nutrition Lab, Washington State University, Pullman, WA, USA) and an equation developed for wild ungulates (Robbins et al. 1987a, 1987b, Hanley et al. 1992). We then converted dry matter digestibility values to digestible energy (DE; Cook et al. 2016) measured as kcal/g.



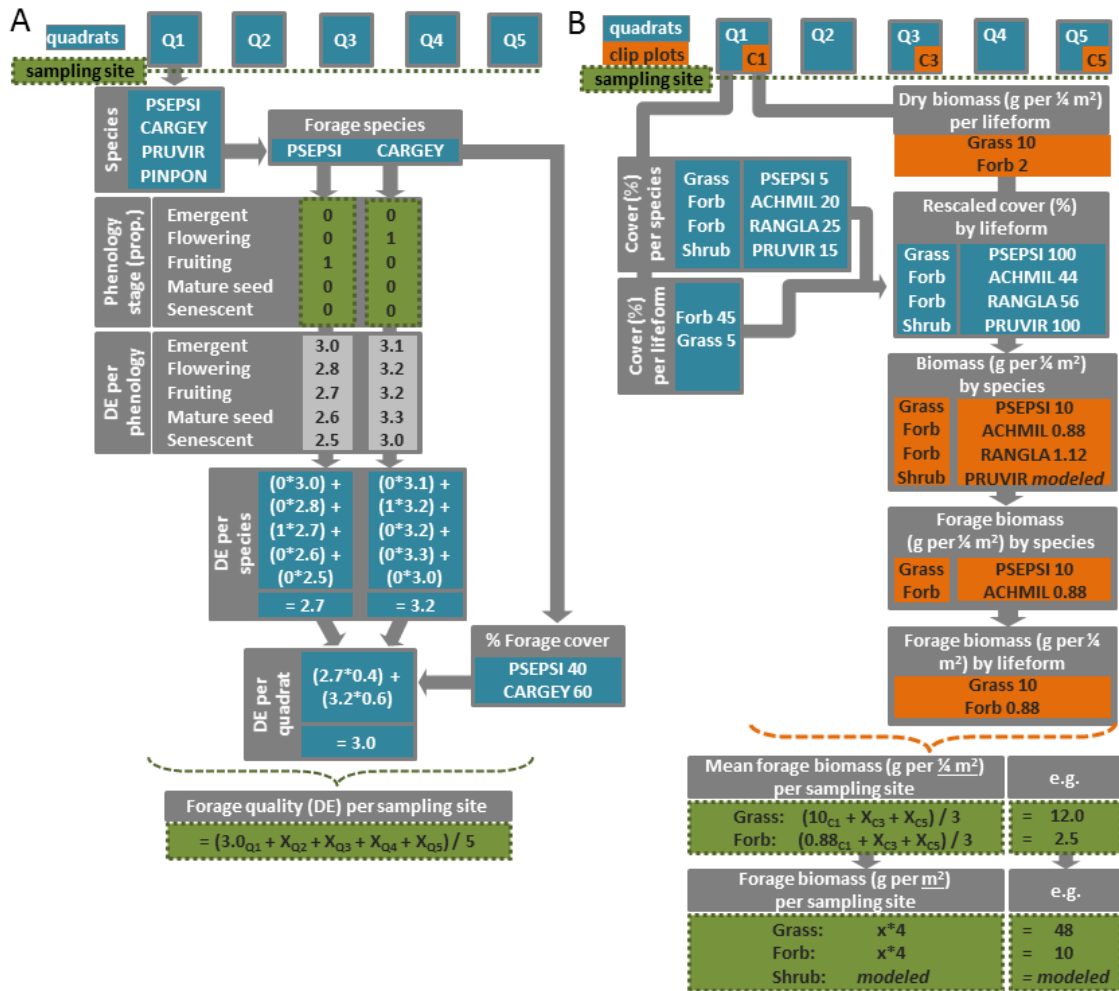
To estimate forage quality within each sampling quadrat at each sampling site, we first rescaled forage species percent cover to estimate the proportion of each forage species in each phenological stage, such that the total summed to 1.0. For the summer data, we used the proportion cover (i.e., availability) and phenological stage-specific DE estimates for each forage species to estimate the mean DE of forage species by calculating a weighted mean DE using rescaled proportion cover as the weight. Then, we estimated DE per sampling site as the mean of the 5 quadrat DE estimates within each sampling site, and refer to this value as the forage quality per sampling site (i.e., mean DE; Panel A, Figure 5.2).

To estimate forage abundance ( $\text{g/m}^2$ ) at each sampling site, we first apportioned clipped, dry biomass ( $\text{g}/0.25 \text{ m}^2$ ) for each lifeform to each species based on rescaled percent cover (species cover proportional to cover within the appropriate lifeform). Second, we filtered out forage species and summed biomass across lifeform. Finally, we estimated mean forage abundance at each sampling site by averaging biomass per lifeform across clip plots and scaling up to square meters ( $0.25 \text{ m}^2 \times 4 = 1 \text{ m}^2$ ; Panel B, Figure 5.2).

#### Landscape modeling of forage abundance and quality

We developed landscape nutrition models that predicted summer forage quality and abundance. We used linear models to predict forage quality as a function of spatial covariates. We used log-linear models to predict forage abundance as a function of spatial covariates, and we treated forb, graminoid, and shrub forage abundance as separate models. We evaluated 8 standardized spatial covariates as predictors of forage quality and abundance: vegetation cover class, elevation, slope, canopy cover, compound topography index (CTI), solar radiation index, spring precipitation (PRISM Climate Group 2016), and NDVI amplitude. We used annual variations in spring precipitation and NDVI amplitude covariates to account for annual variations in growing season conditions during the 4 years of vegetation sampling. We selected the top





**Figure 5.2. Methods for estimating a) mean forage quality (i.e., digestible energy; kcal/g) and b) mean forage abundance (g/m<sup>2</sup>) at each vegetation sampling site.**

ranked models of forage quality and abundance using backwards-stepwise model selection, and we used  $P = 0.05$  as the threshold for inclusion or exclusion of predictor variables. We summed the predicted forb and graminoid forage abundance estimates into an estimate of herbaceous forage abundance.

### Wildfire- and prescribed fire-induced variability in nutritional resources, 1900–2015

To investigate the effects of wildfire on forage during the past century, we used historical wildfire data and our landscape nutrition models to predict summer forage quality and abundance each decade from 1900–2015. Wildfire and prescribed fire history data included previously compiled data from 1889–1985 (Gibson et al. 2014) and data compiled as part of this project from 1985–2015. Prescribed fire history data ranged from 1999–2015. For each decade, we developed spatial data representing the time since fire and incorporated these data into our land cover model. Using these decadal land cover products to classify vegetation cover type, we used the estimated coefficients from our top-ranked models to predict forage quality and abun-

dance over time. We present decadal percent of the elk population summer range predicted to be within each of 4 nutritional value classes for lactating female elk in summer and early autumn based on studies performed by Cook et al. (2004, 2016): excellent (DE  $\geq 2.90$  kcal/g; no nutritional limitations), good (DE 2.75–2.89 kcal/g; minor nutritional limitations on reproductive and survival performance), marginal (DE 2.40–2.74 kcal/g; significant limitation on reproductive performance), and poor ( $\leq 2.39$  kcal/g; significant limitation on reproductive and survival performance).

We used elk location data (see Section 8) collected from collared adult female elk to estimate summer ranges for 3 populations within the study area. We used the summer range boundaries to estimate forage quality and abundance available to elk in each population over time.

## Results

### Elk forage species and vegetation sampling

We collected 26, 21, and 21 composite diet samples from within the North Sapphire, East Fork, and West Fork elk population ranges, respectively. A total of 48, 20, and 18 species comprised 95% of the summer diets for the North Sapphire, East Fork, and West Fork elk populations, respectively (Table 5.1). The most common summer graminoid forage species across all populations were *Poa* spp. and *Carex* spp., comprising 18.0–37.6% of the diets. *Agropyron* spp.,

**Table 5.1. Forage species in the elk summer diet. The percent composition, rank, and cumulative percent of the total diet for the North Sapphire, East Fork, and West Fork elk populations. We considered the species comprising 95% of the cumulative diet from each elk population as summer forage species.**

Species	Life form	North Sapphire			East Fork			West Fork		
		%	Rank	Cum.%	%	Rank	Cum.%	%	Rank	Cum.%
<i>Poa</i> spp.	graminoid	12.1	1	12.1	8.8	4	46.5	11.2	2	37.6
<i>Agropyron</i> spp.	graminoid	8.9	2	20.9	---	---	---	---	---	---
<i>Lupinus</i> spp.	forb	6.2	3	27.1	12.1	2	28.7	7.2	3	44.8
<i>Carex</i> spp.	graminoid	5.9	4	33	16.6	1	16.6	26.4	1	26.4
<i>Verbascum</i> spp.	forb	4.7	5	37.7	0	69	99.9	0	68	100.1
<i>Bromus tectorum</i>	graminoid	4.1	6	41.9	---	---	---	---	---	---
<i>Stipa comata</i>	graminoid	3.1	7	45	---	---	---	---	---	---
<i>Festuca campestris</i>	graminoid	3.1	8	48.1	3.2	10	73.1	0.5	24	95.9
<i>Poa pratensis</i>	graminoid	2.7	9	50.8	---	---	---	---	---	---
<i>Balsamorhiza sagittata</i>	forb	2.6	10	53.4	4	9	69.9	5.5	7	67.4
<i>Medicago sativa</i>	forb	2.4	11	55.8	---	---	---	---	---	---
<i>Salix</i> spp. stem	shrub	2.4	12	58.1	2.1	14	83.4	1.7	14	87.3
<i>Elymus glaucus</i>	graminoid	2.2	13	60.3	---	---	---	---	---	---
<i>Centaurea stoebe</i>	forb	2.1	14	62.5	0	54	99.9	0	48	100.1
<i>Bromus inermis</i>	graminoid	2.1	15	64.6	---	---	---	---	---	---
Other Grass*	graminoid	1.7	16	66.3	4.3	7	61.7	4.4	8	71.8
<i>Festuca idahoensis</i>	graminoid	1.6	17	67.9	1.7	17	88.8	1.2	16	90.1
<i>Shepherdia canadensis</i> leaf	shrub	1.6	18	69.5	---	---	---	---	---	---

\* General grouping category of unidentifiable species in diet analysis not included to screen data

Table 5.1 Continued.

Species	Life form	North Sapphire			East Fork			West Fork		
		%	Rank	Cum.%	%	Rank	Cum.%	%	Rank	Cum.%
Physocarpus malvaceus	shrub	1.5	19	71.1	---	---	---	---	---	---
Calamagrostis rubescens	graminoid	1.5	20	72.6	---	---	---	---	---	---
Other Forb*	forb	1.5	21	74.1	5.5	5	52	5.5	6	61.9
Pseudoroegneria spicata	graminoid	1.5	22	75.5	9	3	37.7	5.8	4	50.6
Composite hair*	---	1.2	23	76.8	1.1	19	91.3	2.7	11	82
Pinus spp.	tree	1.2	24	78	---	---	---	---	---	---
Vaccinium spp. stem	shrub	1.1	25	79.1	1.3	18	90.2	0.7	21	94.1
Achillea millefolium	forb	1	26	80.1	0.1	42	99.4	1.8	12	83.9
Phleum pratense	graminoid	1	27	81.1	---	---	---	---	---	---
Cirsium spp.	forb	1	28	82.2	---	---	---	---	---	---
Astragalus spp.	forb	0.8	29	83	0.3	29	96.8	0.7	19	92.7
Trifolium spp.	forb	0.8	30	83.8	---	---	---	---	---	---
Alopecurus spp.	graminoid	0.7	31	84.6	---	---	---	---	---	---
Taraxacum spp.	forb	0.7	32	85.3	---	---	---	---	---	---
Koeleria macrantha	graminoid	0.7	33	86	0.4	25	95.5	0.4	28	97.6
Other Shrub leaf*	shrub	0.6	34	86.6	0.7	22	93.8	0.4	29	98
Galium spp.	forb	0.6	35	87.2	---	---	---	---	---	---
Ranunculus spp.	forb	0.6	36	87.8	---	---	---	---	---	---
Solidago spp.	forb	0.6	37	88.4	0	67	99.9	0	65	100.1
Other Shrub stem*	shrub	0.5	38	89	0.2	39	99	0.3	32	98.9
Agropyron cristatum	graminoid	0.5	39	89.5	---	---	---	---	---	---
Equisetum spp.	forb	0.5	40	89.9	0.4	26	95.9	1.7	13	85.6
Populus spp. stem	tree	0.5	41	90.4	---	---	---	---	---	---
Potentilla spp.	forb	0.5	42	90.9	0	63	99.9	0	60	100.1
Symphoricarpos albus	shrub	0.5	43	91.4	0.9	21	93.1	0.4	27	97.2
Berberis repens leaf	shrub	0.4	44	91.8	5.5	6	57.5	4.4	9	76.2
Dactylis glomerata	graminoid	0.4	45	92.3	---	---	---	---	---	---
Salix spp. leaf	shrub	0.4	46	92.7	0.3	28	96.6	0.5	26	96.8
Zea mays	graminoid	0.4	47	93.1	---	---	---	---	---	---
Phlox spp.	forb	0.4	48	93.4	0.2	33	97.9	0.5	25	96.4
Cornus spp. leaf	unknown	0.3	49	93.7	0.3	31	97.4	0	49	100.1
Aristida purpurea	graminoid	0.3	50	94	---	---	---	---	---	---
Xerophyllum tenax	forb	0.3	51	94.3	2.8	11	76	0	69	100.1
Prunus spp. leaf	shrub	0.3	52	94.7	---	---	---	---	---	---
Triticum aestivum	graminoid	0.3	53	94.9	---	---	---	---	---	---
Chamerion angustifolium	forb	0.2	54	95.2	0.6	24	95.1	0.7	22	94.8
Juncus spp.	graminoid	0.1	76	98.8	0.9	20	92.2	0.7	20	93.4
Shepherdia canadensis	shrub	---	---	---	4.2	8	65.9	0.6	23	95.4
Other Shrub*	shrub	---	---	---	2.7	12	78.6	3.2	10	79.3
Pinus contorta	tree	---	---	---	2.7	13	81.3	5.8	5	56.4
Stipa spp.	graminoid	---	---	---	1.9	15	85.3	1.6	15	88.9
Bromus spp.	graminoid	---	---	---	1.8	16	87.1	1.1	17	91.1
Physocarpus malvaceus	shrub	---	---	---	0.7	23	94.5	0.2	35	99.5
Ceanothus velutinus	shrub	---	---	---	0.2	41	99.3	0.8	18	92

\* General grouping category of unidentifiable species in diet analysis not included to screen data

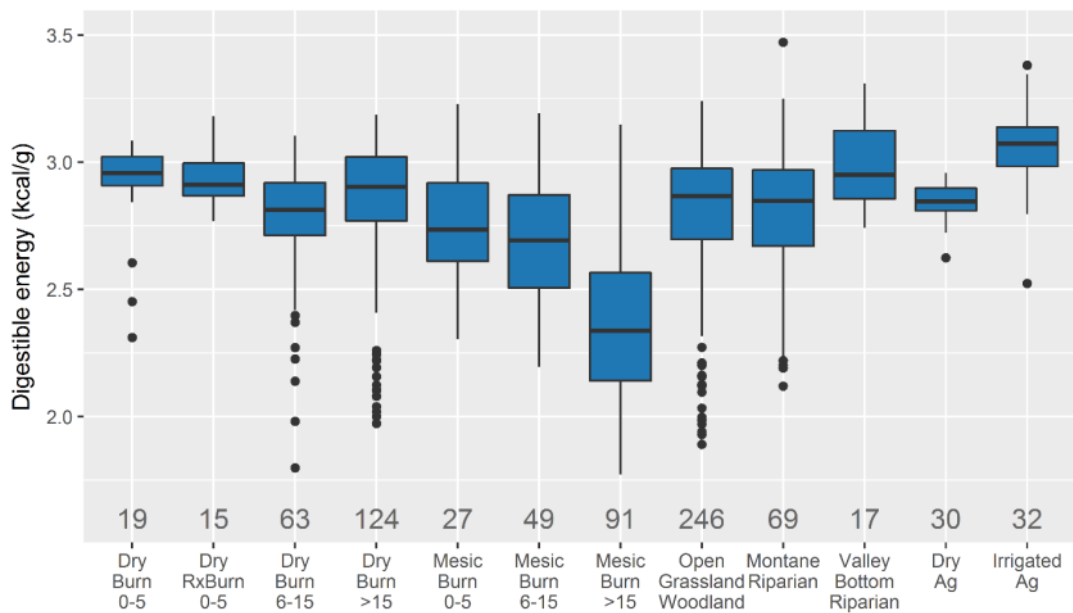
*Bromus tectorum*, and *Stipa comata* were relatively common only to the North Sapphire diet, comprising 16.1% of the diet. The most common summer forb forage species across all populations were *Lupinus* spp. and *Balsamorhiza sagittata*, comprising 8.8–16.1% of the diets. *Verbascum* spp. and *Medicago sativa* were relatively common only to the North Sapphire diet, comprising 7.1% of the diet. The most common summer shrub forage species across all populations were *Salix* spp. and *Vaccinium* spp., comprising 2.9–3.7% of the diets. *Shepherdia canadensis* and *Physocarpus malvaceus* were relatively common only to the North Sapphire diet, comprising 3.1% of the diet.



We sampled vegetation at a total of 752 sites, of which 459, 208, and 111 fell in the North Sapphire, East Fork, and West Fork population ranges, respectively (some sites overlapped population ranges). The most common forb forage species included *Achillea millefolium* (n = 254), *Centaurea stoebe* (n = 160), and *Chamerion angustifolium* (n = 133). The most common graminoid forage species included *Carex geyeri* (n = 280), *Calamagrostis rubescens* (n = 201), and *Pseudoroegneria spicata* (n = 197). The most common shrub forage species included *Symphoricarpos albus* (n = 243), *Berberis repens* (n = 177), and *Vaccinium scoparium* (n = 167). Within late-successional dry forests, the most common forage species included *Carex geyeri* (n = 71), *Symphoricarpos albus* (n = 68), and *Calamagrostis rubescens* (n = 60). Within early-successional dry forests, the most common forage species included *Berberis repens* (n = 13), *Chamerion angustifolium* (n = 11), and *Calamagrostis rubescens* (n = 9). Within early-successional dry forests burned by prescribed fire, the most common forage species included *Achillea millefolium* (n = 10), *Carex geyeri* (n = 10), and *Pseudoroegneria spicata* (n = 9). Within mid-successional dry forests, the most common forage species included *Achillea millefolium* (n = 42), *Symphoricarpos albus* (n = 41), and *Centaurea stoebe* (n = 37). Within late-successional mesic forests, the most common forage species included *Vaccinium scoparium* (n = 55), *Carex geyeri* (n = 47), and *Xerophyllum tenax* (n = 45). Within early-successional mesic forest, the most common forage species included *Chamerion angustifolium* (n = 22), *Vaccinium scoparium* (n = 19), and *Vaccinium membranaceum* (n = 13). Within mid-successional mesic forest, the most common forage species included *Carex geyeri* (n = 32), *Vaccinium scoparium* (n = 31), and *Chamerion angustifolium* (n = 30).

#### Elk forage quality

We collected an average of 7 forage plant samples per species per phenological stage from 34 species in 5 phenological stages and estimated DE. Digestible energy for all forage plants averaged  $2.92 \pm 0.40$  kcal/g ( $\pm$  SD) and varied by plant species, lifeform, and phenological stage. The mean DE estimated at all sampling sites was  $2.76 \pm 0.34$  kcal/g. Estimated mean DE varied across sampling sites located in different vegetation cover classes (Figure 5.3). Digestible energy was highest in irrigated agricultural areas and lowest in late-successional mesic forests.



**Figure 5.3.** Summer mean digestible energy (i.e., forage quality; kcal/g) measured within each vegetation cover class. Horizontal lines through boxes represent median values, the length of the box represents the middle 50% of observations (IQR), vertical lines represent observations within 1.5x the range of the IQR, and points outside the vertical lines represent observations > 1.5x the range of the IQR. Numbers at bottom of plot indicate sample size per cover class. Note different y-axis scales.

Digestible energy was least variable in dry agricultural areas and early-successional dry forests burned by prescribed fire and most variable in valley bottom riparian areas and late-successional mesic forests. Within both mesic and dry forest cover types, variation in DE increased with successional stage.

The top-ranked model predicting forage quality included the covariates vegetation cover class, slope, canopy cover, solar radiation, and elevation ( $r^2_{adj} = 0.26$ ; Table 5.2, Figure 5.4). Comparison of standardized coefficient estimates revealed that forage quality was highest in early-successional mesic and dry forests, including dry forests burned by prescribed fire, and irrigated agricultural areas; however, confidence intervals overlapped. Forage quality was lowest in late-successional mesic forests and valley bottom riparian areas. Dry forests had 0.3–14.5% higher forage quality than mesic forests across comparable successional stages. Confidence intervals for dry versus mesic forests across comparable successional stages did not overlap only for late-successional stages. Within dry forests, forage quality was highest in early-successional forests, or 8.6 and 4.6% higher than mid- and late-successional forests, respectively. Within dry forests burned by wildfire, confidence intervals overlapped slightly for early- and late-successional dry forests. Early-successional dry forests treated with prescribed fire had 2.9% lower and 1.5% higher forage quality, as compared to early and late-successional dry forests burned by wildfire, respectively, however confidence intervals overlapped. Within mesic forests, forage quality was highest in early-successional forests, or 6.6 and 17.2% greater than mid- and late-successional forests, respectively, and confidence intervals overlapped slightly for



early- and mid-successional forests. Forage quality increased with increasing slope and solar radiation index and decreasing canopy cover and elevation.

### Elk forage abundance

Median forb, graminoid, and shrub forage abundance were 4.2, 15.4, and 11.8 g/m<sup>2</sup>, respectively, and forage abundance varied across vegetation cover classes and burn history (Figure 5.5). In both the dry forest and mesic forest, median graminoid and forb forage abundance was highest in mid-successional areas, as compared to early- or late-successional areas. In dry forests, variation in graminoid and forb forage abundance increased with successional stage. Median graminoid and forb forage abundance in dry forests treated with prescribed burns was lower than dry forests untreated with prescribed burns. Shrub forage abundance varied widely within and between vegetation cover classes (Panel B, Figure 5.5). In dry forests, median shrub forage abundance was highest in areas treated with prescribed burns. In mesic forests, median shrub forage abundance was highest in late-successional areas. In dry forests, variation in shrub forage abundance was highest in early-successional areas and lowest in mid-successional areas.

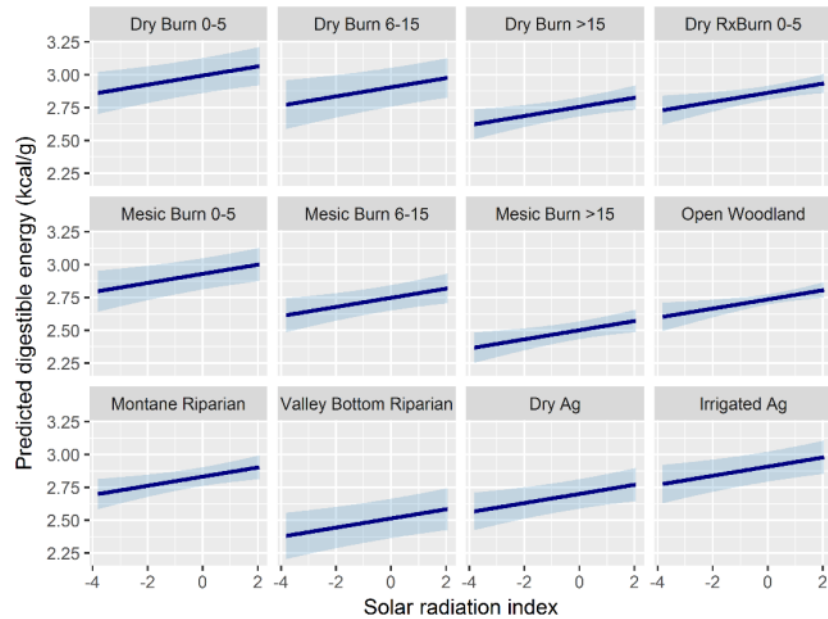
The top-ranked model predicting forb forage abundance included the covariates vegetation cover class, slope, solar radiation, and elevation ( $r^2_{\text{adj}} = 0.17$ ; Table 5.2). Within dry forests, forb abundance was higher in mid-successional areas than in early- or late-successional areas, however confidence intervals overlapped. Dry forests that were treated with prescribed fire had lower forb forage abundance, as compared to early- or late-successional dry forests burned by wildfire, however confidence intervals overlapped. Overall, mesic forests had higher forb abundance than dry forests aside from mid-successional dry forests. In mesic forests, early-successional areas had the highest forb abundance, however, confidence intervals overlapped with mid- and late-successional mesic. Across all cover classes, forb abundance was highest in irrigated agricultural areas and lowest in dry agricultural areas. Forb forage abundance increased as slope, solar radiation, and elevation increased.

The top-ranked model predicting graminoid forage abundance included the covariates vegetation cover class, CTI, canopy cover, NDVI

**Table 5.2. Standardized coefficient estimates for the top models predicting summer and winter forage quality and forage abundance per life form. Boldface values denote 95% confidence intervals not containing 0. Effects of vegetation cover classes are in relation to the base cover class Dry Forest Burned > 15 years prior.**

Covariate	Forage quality	Forage abundance		
		Forb	Gram.	Shrub
Intercept	<b>2.86</b>	-0.29	<b>2.59</b>	<b>1.32</b>
Dry Forest Burn 0-5	0.13	-0.70	-0.19	-0.62
Dry Forest Rx Burn 0-5	0.04	-0.38	-0.63	<b>1.90</b>
Dry Forest Burn 6-15	<b>-0.11</b>	<b>2.23</b>	0.003	<b>2.71</b>
Mesic Forest Burn >15	<b>-0.36</b>	<b>1.21</b>	<b>-1.63</b>	0.58
Mesic Forest Burn 0-5	0.07	<b>1.58</b>	-0.07	<b>-2.15</b>
Mesic Forest Burn 6-15	<b>-0.11</b>	0.93	-0.19	<b>1.11</b>
Grass/Shrub/Open Woodland	<b>-0.13</b>	<b>0.75</b>	-0.46	<b>-1.58</b>
Montane Riparian	-0.03	<b>1.43</b>	<b>-0.82</b>	-0.73
Valley Bottom Riparian	<b>-0.35</b>	0.64	<b>-1.57</b>	<b>-1.85</b>
Dry agriculture	<b>-0.16</b>	<b>-1.10</b>	-0.24	<b>-3.62</b>
Irrigated agriculture	0.05	<b>3.12</b>	<b>-1.96</b>	<b>-3.89</b>
Solar Radiation	0.03	<b>0.68</b>	<b>0.59</b>	0.20
Canopy Cover	<b>-0.08</b>	-	<b>-0.59</b>	<b>1.78</b>
Slope	0.02	0.21	-	-
Elevation	<b>-0.08</b>	<b>0.58</b>	<b>-0.71</b>	-
Compound Topo. Index	-	-	-0.13	-
NDVI amplitude	-	-	0.18	-

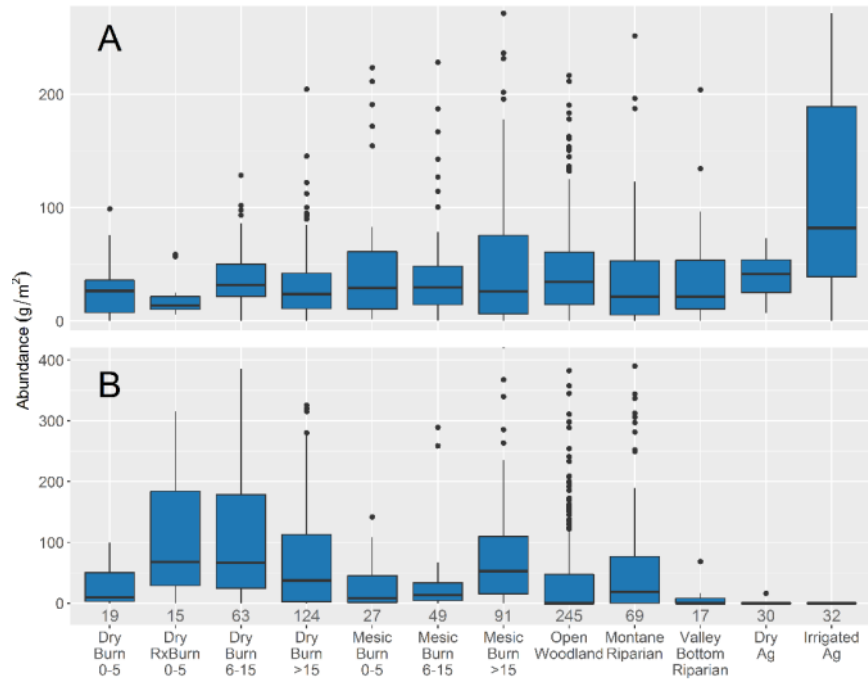
amplitude, solar radiation, and elevation ( $r^2_{\text{adj}} = 0.22$ ; Table 5.2). Dry and mesic forests had similar graminoid abundance excepting late-successional dry forests with lower predicted abundance than all other forest cover types. In dry forests, predicted graminoid abundance was similar across all burn histories. Dry forests that were treated with prescribed fire had lower graminoid forage abundance, as compared to early- or mid-successional dry forests burned by wildfire, however confidence intervals overlapped. In mesic forests, late-successional areas had lower predicted graminoid forage abundance than early- or mid-successional areas. Across all cover classes, graminoid abundance was lowest in irrigated agricultural areas and valley bottom riparian areas and highest in mid- and late-successional dry forests. Graminoid forage abundance increased as CTI, canopy cover, and elevation decreased and increased as NDVI amplitude and solar radiation increased.



**Figure 5.4.** Predicted summer digestible energy for each vegetation cover class across the observed range of solar radiation index values based on predictions from the top ranked models (holding other covariates at their mean value). The lines represent the mean predicted digestible energy and the shaded bands represent the 95% confidence interval.

Herbaceous forage abundance predictions (combined forb and graminoid model predictions) varied by vegetation cover class. Dry forests had 58.7–174.0% greater herbaceous forage abundance than mesic forests across comparable successional stages, excepting early-successional areas, where mesic forests had 21.7% greater abundance. Within dry forests, herbaceous forage abundance was highest in mid-successional forests, or 44.5% greater than late-successional forests. Dry forests that were treated with prescribed fire had 39.6 and 46.1% lower herbaceous forage abundance than early- or late-successional areas burned by wildfire, respectively. Within mesic forests, herbaceous forage abundance was highest in early-successional forests, or 211.9% greater than late-successional forests.

The top-ranked model predicting shrub forage abundance included the covariates vegetation cover class, canopy cover, and solar radiation ( $r^2_{\text{adj}} = 0.41$ ; Table 5.2). Within dry forests, shrub abundance was highest in mid-successional areas, or 1409.1% greater abundance than late-successional areas. Dry forests that were treated with prescribed fire also had high shrub forage abundance, or 1139.9 and 566.4% greater abundance than early- and late-successional areas burned by wildfire, respectively. Within mesic forests, early-successional areas had lower



**Figure 5.5.** The mean herbaceous (panel A) and shrub (panel B) forage abundance ( $\text{g}/\text{m}^2$ ) measured within each vegetation cover class. Horizontal lines through boxes represent median values, the length of the box represents the middle 50% of observations (IQR), vertical lines represent observations within 1.5x the range of the IQR, and points outside the vertical lines represent observations >1.5x the range of the IQR. Numbers at bottom of plot indicate sample size per cover class. Note different y-axis scales.

shrub forage abundance than mid- or late-successional mesic forests, or 96.2 and 93.5% lower abundance, respectively. Shrub forage abundance increased as canopy cover and solar radiation increased.

#### Estimated fire-induced variability in nutritional resources, 1900–2015

We estimated the area of summer ranges to be 775, 1,728, and 645  $\text{km}^2$  in the North Sapphire, East Fork, and West Fork populations, respectively. The total area burned per decade varied during 1900–2015, and averaged 24.5, 90.2, and 34.1  $\text{km}^2$  within the North Sapphire, East Fork, and West Fork summer ranges, respectively. The area burned during 1900–1990 was low and had little variation across time or populations, averaging 17.4, 16.2, and 7.3  $\text{km}^2$  per decade in the North Sapphire, East Fork, and West Fork summer ranges, respectively. From 1990–2015, the average area burned per decade increased 242%, 1,772%, and 1,315% compared to 1900–1990 to 42.1, 287.2, and 96.0  $\text{km}^2$  in the North Sapphire, East Fork, and West Fork summer ranges, respectively. Overall, the largest area burned occurred in the East Fork summer range during 1991–2000 with 41.5% and 1.5% of the range burned by wildfire and prescribed fire, respectively. In the North Sapphire summer range, the largest area burned occurred during 2001–2010 with 11.6% and 1.6% of the range burned by wildfire and prescribed fire, respectively. In the West Fork summer range, the largest area burned occurred during 1991–2000 with 20.1% and 4.9% of the range burned by wildfire and prescribed fire, respectively.

The percent of summer range in dry and mesic forest burn history classes within each population did not vary substantially across 1891–1990 (Figure 5.6). The average percent of summer range in early- and mid-successional mesic forests across populations increased 4.5–16.3 times from 0.8–1.3% during 1891–1990 to 3.6–16.3% during 1991–2015. The average percent of summer range in early- and mid-successional dry forests was slightly more variable across populations than for mesic forests, increasing 2.5–26.4 times from 0.7–1.9% to 4.7–18.1% for the same decades. Open grasslands, shrublands, and woodlands were a dominant cover type in the summer ranges, comprising 30.7, 29.1, and 17.4% of the North Sapphire, East Fork, and West Fork, respectively. Irrigated agricultural areas were only present in the North Sapphire and comprised 3.0% of the summer range. Dry agricultural areas comprised 3.0, 1.3, and 0.1% of the North Sapphire, East Fork, and West Fork summer ranges, respectively. Montane riparian cover types comprised 7.6, 10.2, and 7.9% of the North Sapphire, East Fork, and West Fork summer ranges, respectively. Remaining cover types were of low proportion of summer range.

The percent of the elk summer ranges comprised of good and marginal nutritional value classes did not vary substantially during 1891–2015, averaging 45.1 and 26.8%, 40.7 and 34.0%, and 30.9 and 44.2% in the North Sapphire, East Fork, and West Fork, respectively (Figure 5.6).

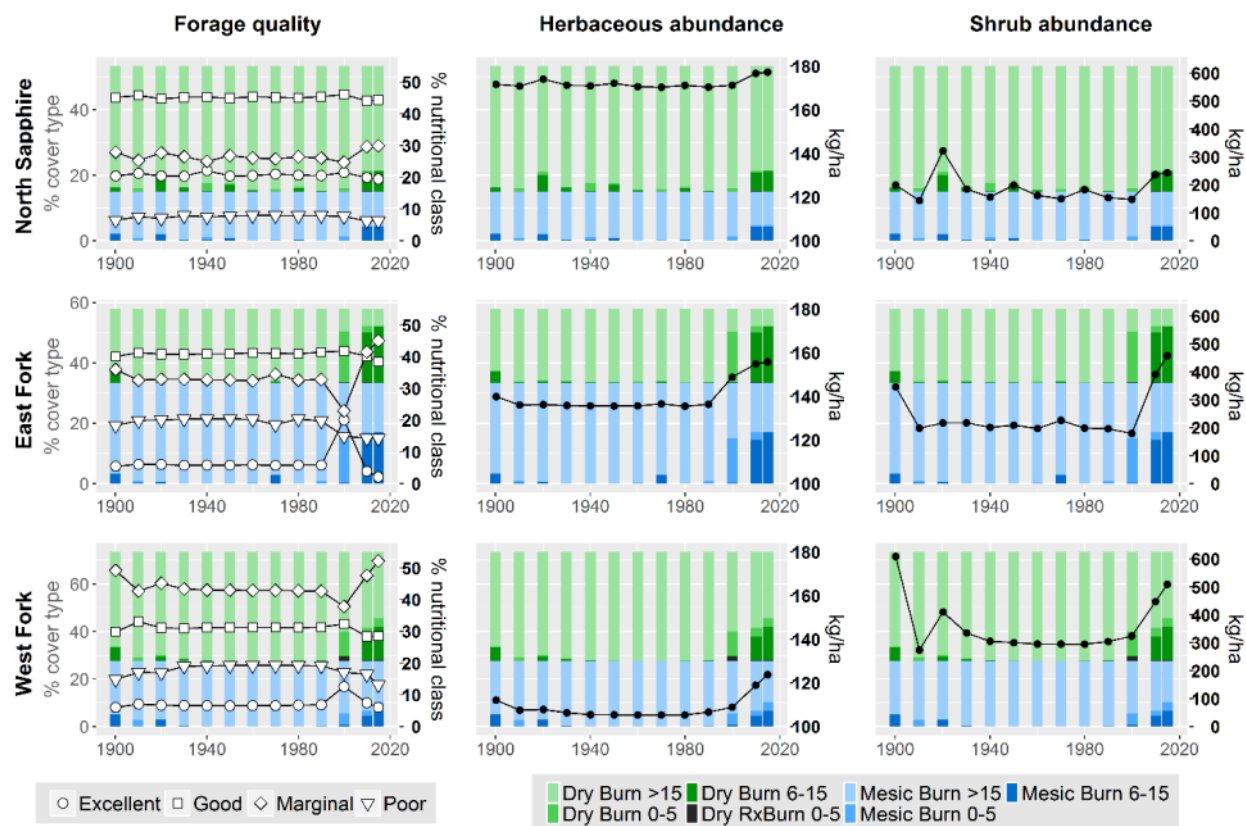


Figure 5.6. The percent area of dry and mesic forest cover types burned per decade (color shaded bars) and predicted percent area of each nutritional value class (white symbols), herbaceous forage abundance (black dots), and shrub forage abundance (black dots) within the North Sapphire (775 km<sup>2</sup>), East Fork (1,728 km<sup>2</sup>), and West Fork (645 km<sup>2</sup>) elk population summer ranges. Note different left-hand (% cover type) y-axis scales.

Within the North Sapphire, the amount of excellent and poor nutritional value classes also varied insubstantially during this period, averaging 20.7 and 7.4%, respectively. The East Fork and West Fork summer ranges experienced greater variation during 1991–2015 as compared to the previous decades. These summer ranges increased approximately 2.8 and 2.1% in the amount of excellent nutritional value class, respectively, rising from an average of 5.8 and 6.6% during 1891–1990 to 8.7 and 8.7% during 1991–2015, respectively. During these same decades, the amount of poor nutritional value class in the East Fork and West Fork declined approximately 5.3 and 2.7%, respectively, from 19.8 and 18.3% to 14.5 and 15.6%.

Herbaceous forage abundance per decade did not vary substantially during 1891–1990, averaging 171.4, 136.3, and 106.7 kg/ha in the North Sapphire, East Fork, and West Fork summer ranges, respectively (Figure 5.6). During 1991–2015, herbaceous forage abundance increased 2.2, 12.4, and 9.8% to an average of 175.1, 153.2, and 117.2 kg/ha in the North Sapphire, East Fork and West Fork summer ranges, respectively. For all elk populations, the highest herbaceous forage abundance occurred in the half-decade 2011–2015.

## Discussion

We found that wildfire and prescribed fire had important yet dissimilar effects on elk forage quality and abundance. Our results show that large-scale temporal and spatial variations in wildfire activity has the potential to alter elk nutritional resources, and that the effects of wildfire on nutritional resources vary across elk populations as a function of terrain and forest cover types burned. Our findings highlight the varying effects of forest type, wildfire, prescribed fire, and age of burn on forage quality and abundance. Additionally, together with other studies (Cook et al. 2013, 2016, Proffitt et al. 2016a, 2016b), our results suggest that forage quality, and fire-related variability in forage quality, may affect elk nutritional condition and reproductive performance.

We found that prescribed fires within our study area did not mimic the effect of natural wildfires, and may result in short-term reductions in forage quality and abundance. In early-successional dry forests burned by prescribed fire, forage quality and herbaceous forage abundance was lower than early-successional dry forests burned by wildfire. Shrub forage abundance was greater in areas burned by prescribed fire as compared to wildfire; however, shrub forage species had relatively low importance in elk diets. Our results are similar to Long et al. (2008), who found no difference in herbaceous forage quality, lower herbaceous forage cover, and higher shrub forage cover in coniferous forest stands thinned and burned by prescribed fire as compared to untreated stands. Together, these results suggest that dry forests in late-successional stages likely provide better forage opportunities than early-successional areas treated with prescribed burns.

The observed difference in effect of prescribed fire and wildfire may be due to the restriction of prescribed burns to specific times of year, reduced severity of prescribed fire, or other factors purposefully managed to prevent unintentional conflagrations causing collateral damage to adjacent forests habitats, human developments, and private lands (Ryan et al. 2013). Land managers should consider that while prescribed burns may be valuable for other



purposes (e.g., reducing excessive fuels, returning forests to a semblance of historical ecological conditions; Arno et al. 2000, Ryan et al. 2013), or enhancing nutritional resources in aspen forests (Canon et al. 1987), our study lends little evidence to support using prescribed fire for enhancement of summer nutritional resources in coniferous forests. Additionally, because of their relatively small scale use, prescribed fires likely have a small effect on ungulate nutritional resources. Our study did not evaluate effects of prescribed fire on nutritional resources in grassland, shrubland, or open woodland communities, but nutritional resources may or may not be enhanced and selected for by elk in these areas (Jourdonnais and Bedunah 1990, Peck and Peek 1991, Vore et al. 2007, Sittler et al. 2015).



We found evidence for generally enhanced summer nutritional resources as a consequence of wildfire, but the effect varied depending on forest type and post-fire successional stage, similar to results presented in Proffitt et al. (2016a, 2016b). Dry forests were predicted to have better nutritional resources than mesic forests across the same relative post-fire successional stages, with two exceptions. Mesic forests were predicted to have higher herbaceous forage abundance in early-successional stages and higher shrub forage abundance in late-successional stages as compared to dry forests in the same relative successional stage. Additionally, within dry forests there was an inverse relationship between forage quality and abundance (Hebblewhite et al. 2009) within each successional stage. In dry forests, early-successional stages experienced the highest forage quality and a marginal decrease of forage abundance. Mid-successional stages experienced the lowest forage quality and the highest forage abundance. In mesic forests, early-successional stages experienced the highest of both forage quality and herbaceous forage abundance. Mid-successional stages experienced a decrease of both forage quality and herbaceous forage abundance (but levels remained higher than late-successional levels).

During the past century, the predicted fire-related availability of elk nutritional resources varied across time and by population range (Figure 5.6). These wildfire-induced changes in nutritional resources can be directly related to the historical large-scale changes in federal wildland fire policy across the Rocky Mountains (Arno 1976, Rollins et al. 2001). Prior to modern forestry management, the forests in this study region experienced relatively frequent fires of low to medium severity during 1735–1900, with lower elevation Douglas-fir/ponderosa pine forests (i.e., dry forests) experiencing fire approximately every 10 years and higher elevation subalpine fir and lodgepole pine forests (i.e., mesic forests) experiencing fire approximately every 20–30 years (Arno 1976). Because of changes in forest management that began in the early 1900s and included broad-scale wildfire suppression, a marked decrease in frequency, size, and severity of wildfires occurred in this area (Arno 1976, Rollins et al. 2001), likely resulting in late-successional forest stands with lower ungulate nutritional resources. Beginning

around 1975, federal policy began shifting away from suppression strategies that resulted in fuel accumulation and larger, more severe fires (Arno et al. 2000) and towards using wildland fire to benefit resources. The lasting consequences of the suppression era, combined with increasing use of wildfires to maintain or enhance natural resources, are reflected in our study populations with substantial increases in area burned in decades 1991–2015. During this period, all populations experienced predicted increases in herbaceous and shrub forage abundance on summer ranges. Forage quality on summer ranges experienced a modest increase to a fire in the decade spanning 1991–2000 occurring in both dry and mesic forest types resulting in a large proportion of early-successional stage forests.

Our study quantified the potential fire-related spatial and temporal variation in elk nutritional resources; however, we did not quantify changes in vegetation cover types resulting from timber harvest, shifting vegetation communities from climate change, or altered land use from human land conversions. It is likely that nutritional resources are more variable depending on the spatial and temporal distribution of these effects, and land and wildlife managers should consider this effect. Timber harvest has been a significant forest management practice in the Bitterroot Valley landscape and may have important effects on elk nutritional resources and habitat selection (Hebblewhite et al. 2009, Cook et al. 2016). For example, some systems may experience short-term increases of nutritional resources in clearcut logged or thinned areas (Cook et al. 2016). However, other studies in Canadian Rockies found lodgepole pine (*Pinus contorta*) and spruce (*Picea engelmanni* and *P. mariana*) forests stands that were logged pre-fire, logged post-fire, and burned-only showed few differences in herbaceous forage abundance after the third year post-fire (Hebblewhite et al. 2009). In recent decades, rates of timber harvest have drastically declined within the Bitterroot Valley, and unburned, late-successional forests may have relic effects from these past timber harvests on elk forage quality and abundance. This may confound our predictions for late-successional forests. In addition to wildfire and timber harvest, other landscape-scale processes such as tree disease and insect infestation may have important effects on nutritional resources. Although there is currently only limited timber harvest, tree disease, or insect-infestation within our study areas, the large-scale effects of these factors may impact nutritional resources in other forest ecosystems, and a better understanding of these effects on ungulate nutritional resources is needed to guide management of forest ecosystems.

Our finding that summer forage quality and herbaceous forage abundance was higher in irrigated agricultural lands as compared to native grasslands or any forested cover class also has important implications for elk management. Irrigated agricultural areas were predicted to have 22.6 times greater forb forage abundance and 2.1 times greater forage quality than late-successional dry forests, 6.7 times greater forb abundance and 10.1 times greater forage quality than late-successional mesic forests, and 4 times greater forage quality and 10.7 times greater forb abundance than open woodland areas. This distribution of abundant, high quality forage throughout the summer in irrigated agricultural areas likely has important effects on elk distributions and contributes to increased resident elk populations that are not dependent on migratory strategies to access high quality nutrition during the summer months. The presence of abundant, high-quality forage in privately owned irrigated agricultural areas may draw elk off

public lands, and, if hunter access to these private lands is restricted, may limit harvest as an effective tool to regulate elk populations within socially tolerable levels (Haggerty and Travis 2006, Proffitt et al. 2013). With land-use changes over time and increases in irrigated agriculture, increasingly resident elk populations may become common, and associated property damage complaints and conflicts with public land hunters are expected to increase. Additional work is needed to determine if habitat treatments strategically implemented on public land may be used as a management tool to increase the abundance of high quality forage and maintain elk distributions across public and private lands

## Section 6 — Relating Remotely-sensed Vegetation Indices to Measures of Elk Forage and Nutrition

### Introduction

Female elk require high quality nutrition during summer to support demands of lactation and calf-rearing while accruing sufficient body fat to survive the nutrient-limited winter months. Females with higher body fat at the end of summer are more likely to become pregnant in the fall, and calves with access to high nutrition during summer exhibit faster growth rates and higher winter survival than calves with inadequate nutrition (Cook et al. 2004). Due to the strong effect of summer nutrition on elk fecundity and survival (Cook et al. 2004a, 2016; see also Section 5), understanding the nutrition available to, and acquired by, elk during summer is important.



Elk nutrition is typically estimated using measurements of either plants (i.e., the nutrition elk are exposed to) or animals (i.e., the nutrition elk have gained from forage). Nutritional measurements of plants can be divided into two main classes: forage quantity, often measured as biomass; and forage quality, often measured as digestibility. Because the quantity and quality of available forage often vary widely across elk summer range, measuring the nutrition elk are exposed to requires extensive vegetation sampling and laboratory work. Because of this constraint, and because plant-based measurements of nutrition may not fully capture nutritional intake of animals, animal-based measurements of nutrition can also be informative. However, animal-based measurements of nutritional condition often prove difficult to obtain. Nitrogen in fecal pellet samples can serve as a reliable estimator of the protein animals gain from forage, but fecal nitrogen decays over time (Wehausen 1995, Leslie et al. 2008, Hamel et al. 2009). Locating and processing sufficient quantities of fresh fecal samples can be time- and resource-intensive.

Remote sensing technology has recently emerged as a potential tool to efficiently estimate nutrition availability for large herbivorous mammals during the growing season (Pettorelli et al. 2011). The Normalized Difference Vegetation Index (NDVI), a remotely sensed index of greenness measured periodically throughout the year, may correlate with measures of vegetation including above-ground biomass (Boelman et al. 2003) and net primary production (Paruelo et al. 1997). Because elk only forage on certain plants, however, indices of biomass or productivity in an area may not accurately represent biomass, digestibility, or productivity of elk forage plants. For example, on the northern Yellowstone elk range, NDVI explained 18% of the variation in digestibility of graminoids in open grassland areas (Garrouette et al. 2016), but the ability of NDVI to serve as a proxy for the quantity or quality of elk forage plants remains undetermined. In addition to relating NDVI to plant-based measures of elk nutrition, several studies have assessed the relationship between NDVI and fecal nitrogen of elk by associating NDVI data with the timing and locations of pellet collections. Relationships quantified to date have varied

widely across both spatial (Martínez-Jauregui et al. 2009) and temporal (Ryan et al. 2012) scales, to such a degree that these relationships must be “recalibrated” for use in any new area (Creech et al. 2016). Thus, we lack a generally applicable model relating NDVI to fecal nitrogen and nutritional exposure of elk.

Though the most popular, NDVI is not the only remotely-sensed vegetation index. The Enhanced Vegetation Index (EVI), calculated similarly to NDVI, is designed to handle factors like cloud cover or wildfire smoke more effectively than NDVI, and unlike NDVI it does not saturate at high levels of greenness (Pettorelli 2013). EVI can correlate well with crude protein content of forage plants in open grassland areas (Garrouste et al. 2016), but correlations in other land cover types remain undescribed. Other remotely-sensed indices provide proxies for vegetative growth throughout an entire growing season, rather than in discrete time intervals. NDVI amplitude, for instance, represents the maximum increase in canopy photosynthetic activity during the growing season. Time-integrated NDVI represents the amount of canopy photosynthetic activity that occurred throughout the growing season. Relationships between NDVI amplitude or time-integrated NDVI and elk nutrition have not been fully explored.

The extent to which remotely-sensed vegetation indices correlate with forage quantity, forage quality, or elk nutritional intake over spatiotemporal scales relevant to elk distributions during summer remains unclear. Thus, our objective was to quantify relationships between remotely-sensed vegetation indices and measurements of elk nutrition in order to assess the general utility of using remotely-sensed data as a proxy for elk nutrition during summer. Specifically, we compared the abilities of 4 remotely-sensed vegetation indices (NDVI, EVI, NDVI amplitude, and time-integrated NDVI) to predict 4 measures related to elk nutrition (forage biomass, herbaceous forage biomass, forage digestibility, and fecal nitrogen).

## Methods

We estimated forage biomass ( $\text{g/m}^2$ ), herbaceous forage biomass (graminoids and forbs only;  $\text{g/m}^2$ ), and digestible energy (DE;  $\text{kcal/g}$ ) based on extensive elk diet and vegetation surveys conducted in the northern Sapphire Mountains during summer 2014 and 2015 (Figure 6.1; see Section 5 for detailed methods). To estimate elk nutritional intake, we collected fresh composite fecal pellet samples from at least 4 sites every 16 days from June–October in 2014 and 2015. We selected sampling sites based on female elk locations recently recorded by Global Positioning System (GPS) collars. Each composite sample consisted of up to 20 fresh (< 48 hour old) pellets collected from 7–10 discrete pellet clusters. We dried samples for at least 48 hours at  $50^\circ\text{C}$  before sending them to the Washington State University Wildlife Habitat Nutrition Laboratory, and we estimated fecal nitrogen content using Dumas combustion analysis.

We used Google Earth Engine to acquire pre-processed NDVI and EVI measured by the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on NASA’s Terra satellite, and we acquired NDVI amplitude and time-integrated NDVI from the USGS EROS Center (<https://phenology.cr.usgs.gov>). NDVI and EVI values were scaled by dividing each value by 0.0001. We extracted NDVI, EVI, NDVI amplitude, and time-integrated NDVI values associated with the locations and sampling times of vegetation plots and fecal pellet sampling locations. We designed

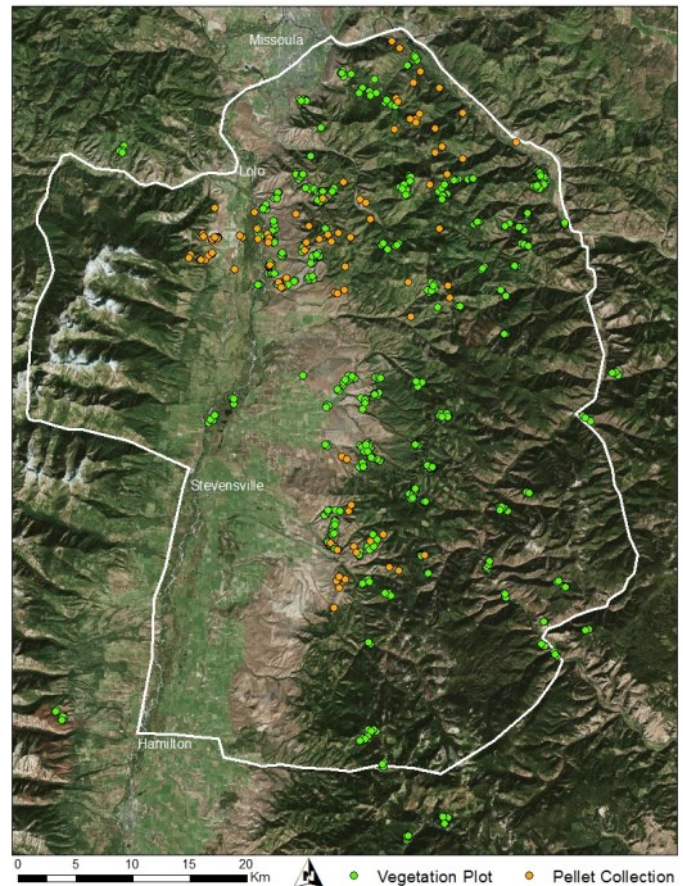


our pellet sampling protocol to correspond closely with the spatial and temporal scales of the NDVI and EVI data (30m<sup>2</sup> and 16 days, respectively).

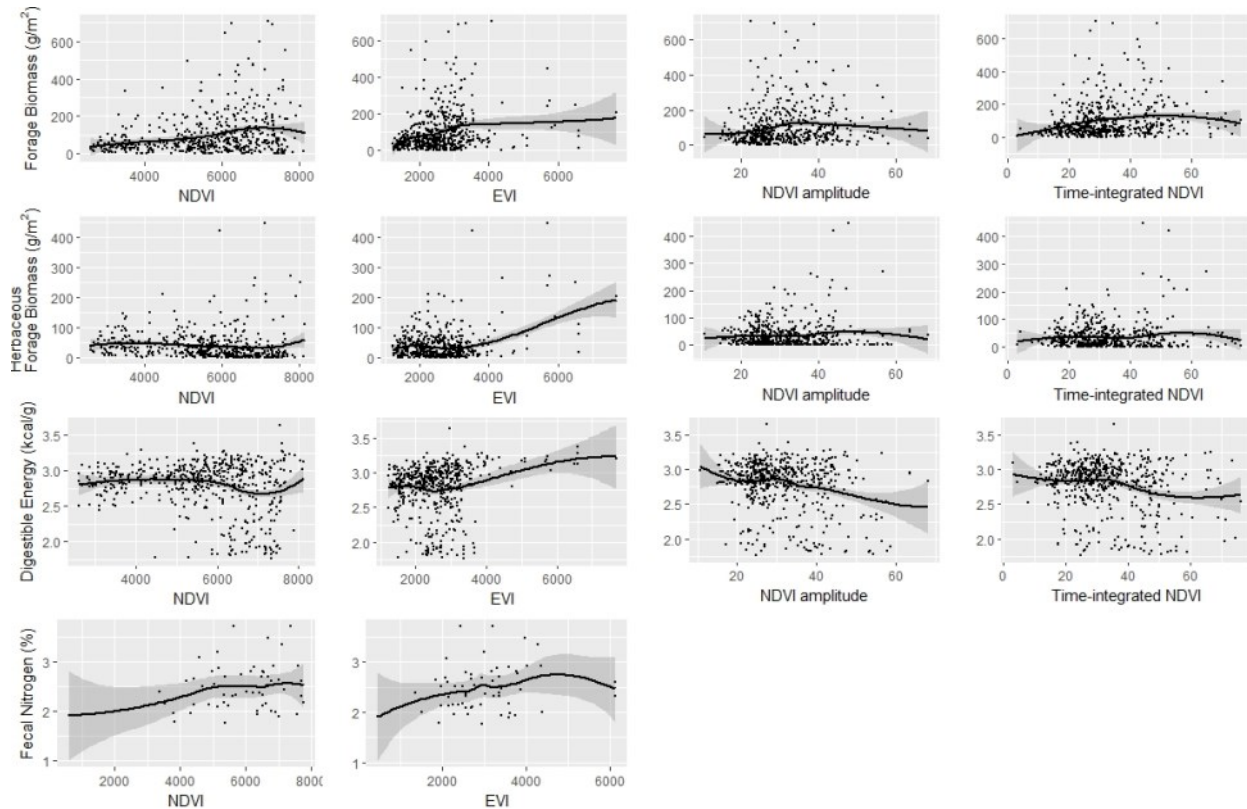
We used linear regression models to quantify the relationship between remotely-sensed vegetation indices and each measure of elk nutrition. We used AICc to compare relative support for models and considered models with  $\Delta AICc > 2$  to be unsupported (Burnham and Anderson 2002). We assessed relative support for NDVI, EVI, NDVI amplitude, and time-integrated NDVI to predict each of the 3 vegetation measurements (forage biomass, herbaceous forage biomass, and digestible energy) as well as fecal nitrogen measurements. We also assessed whether inclusion of polynomial terms (quadratic and cubic) and tree cover appreciably improved predictive ability. For models incorporating tree cover, we included an interaction with a binary variable indicating presence of a forested land cover type. Thus, we assessed relative support for 24 models predicting each vegetation measurement (linear, quadratic, and cubic relationships with each of the 4 remotely-sensed vegetation indices, with and without inclusion of an interaction with tree cover). For fecal nitrogen measurements, we did not consider NDVI amplitude or time-integrated NDVI as potential predictors, because fecal nitrogen was measured periodically throughout the summer whereas NDVI amplitude and time-integrated NDVI represent measurements for the entire growing season. We assessed relative support for 12 models predicting fecal nitrogen (linear, quadratic, and cubic relationships with NDVI and EVI, with and without inclusion of an interaction with tree cover).

## Results

Measures of elk nutrition varied widely across associated values of remotely-sensed vegetation indices (Figure 6.2). We found similar support for 3 models predicting forage biomass, 2 models predicting herbaceous forage biomass, 2 models predicting forage quality, and 3 models predicting fecal nitrogen (Table 6.1; Figure 6.3). None of the forested land cover in our



**Figure 6.1.** Vegetation plots (green) and elk pellet sampling locations (orange). Data collected from vegetation plots was used to estimate the quantity (g/m<sup>2</sup>) and quality (kcal of digestible energy/g) of forage available to elk during the growing season; pellet samples were used to estimate elk nutritional intake (fecal nitrogen, %).



**Figure 6.2.** Locally-weighted smoothed scatterplots illustrating relationships between remotely sensed vegetation indices (x-axes) and measurements related to elk nutrition (y-axes). Measurements of elk nutrition were forage biomass ( $\text{g/m}^2$ ; row 1) herbaceous forage biomass ( $\text{g/m}^2$ ; row 2), digestibility of forage plants (kcal of digestible energy/g of forage; row 3), and elk fecal nitrogen (%; row 4). Remotely-sensed vegetation indices were the Normalized Difference Vegetation Index, a remotely-sensed index of greenness (NDVI; column 1); the Enhanced Vegetation Index, an index similar to NDVI that does not saturate at high levels of greenness (EVI; column 2); NDVI amplitude, canopy photosynthetic activity throughout the growing season (column 3); and time-integrated NDVI, maximum increase in canopy photosynthetic activity during the growing season (column 4).

study area had high EVI values, and an interaction with tree cover improved predictive ability for most models that included EVI.

Top-supported models predicting forage biomass were NDVI, an interaction between EVI and tree cover, and an interaction between quadratic EVI and tree cover ( $p < 0.001$  in all cases). Forested areas were predicted to have higher forage biomass than open canopy areas. Forage biomass tended to increase linearly with increasing NDVI and EVI in both forested and open canopy areas. One supported model indicated forage biomass may decrease with increasing EVI in open canopy areas after EVI exceeds about 6000.

Top-supported models predicting herbaceous forage biomass were an interaction between quadratic EVI and tree cover, and an interaction between cubic EVI and tree cover ( $p < 0.001$  in both cases). Open canopy areas were predicted to have higher herbaceous forage biomass than forested areas. In open canopy areas, herbaceous forage biomass decreased very

**Table 6.1. Top-supported linear models predicting measures of elk nutrition using remotely-sensed vegetation indices.**

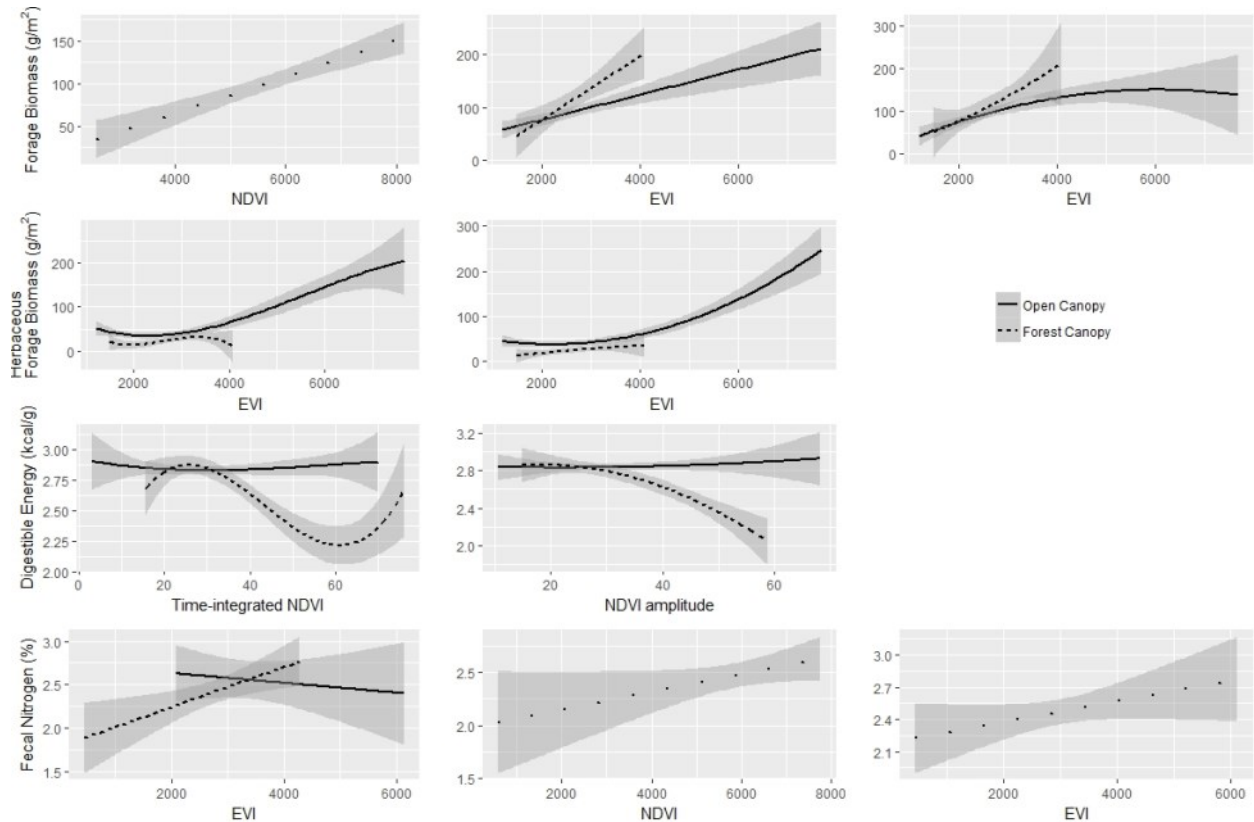
Response Variable	Explanatory Variable(s) <sup>a</sup>	K	AICc	ΔAICc	ω	LL	Adj. r <sup>2</sup>	SE
Forage Biomass (g/m <sup>2</sup> )	NDVI	3	6485.38	0.00	0.27	-3239.67	0.07	105.75
	EVI x Treecover	5	6485.69	0.31	0.23	-3237.79	0.07	105.58
	EVI <sup>2</sup> x Treecover	7	6487.40	2.02	0.10	-3236.60	0.07	105.54
Herbaceous Forage Biomass (g/m <sup>2</sup> )	EVI <sup>3</sup> x Treecover	9	5545.25	0.00	0.52	-2763.45	0.18	43.52
	EVI <sup>2</sup> x Treecover	7	5545.40	0.15	0.48	-2765.59	0.17	43.62
Digestible Energy (kcal/g)	NDVIti <sup>3</sup> x Treecover	9	317.26	0.00	0.56	-149.46	0.14	0.32
	NDVIlamp <sup>2</sup> x Treecover	7	318.43	1.17	0.31	-152.11	0.13	0.32
Fecal nitrogen (%)	EVI x Treecover	5	75.29	0.00	0.29	-32.08	0.09	0.43
	NDVI	3	75.92	0.62	0.21	-34.74	0.04	0.44
	EVI	3	76.83	1.54	0.13	-35.20	0.03	0.45

<sup>a</sup>NDVI refers to the Normalized Difference Vegetation Index, a remotely-sensed index of greenness. EVI refers to the Enhanced Vegetation Index, an index similar to NDVI that does not saturate at high levels of greenness. NDVIti refers to time-integrated NDVI, an index of maximum increase in canopy photosynthetic activity during the growing season. NDVIlamp refers to NDVI amplitude, an index of canopy photosynthetic activity throughout the growing season. Treecover is a binary covariate indicating a forested land cover type.

slightly with increasing EVI until EVI values exceeded about 3000; then, herbaceous forage biomass increased strongly with increasing EVI. In forested areas, the relationship between EVI and herbaceous forage biomass was less clear. Herbaceous forage biomass was predicted either to slightly increase or remain fairly constant with increasing EVI.

Top-supported models predicting forage quality were an interaction between cubic time-integrated NDVI and tree cover, and an interaction between quadratic NDVI amplitude and tree cover ( $p < 0.001$  in both cases). Open canopy areas were typically predicted to have higher forage quality than forested areas. The relationship between forage quality and time-integrated NDVI or NDVI amplitude was very different between open and forested areas. In open canopy areas, forage quality was predicted to remain fairly constant across all values of time-integrated NDVI or NDVI amplitude. In forested areas, forage quality was predicted to decrease with increasing remotely-sensed values at intermediate values of time-integrated NDVI or NDVI amplitude (~30–60). Forage quality in forested areas was predicted to increase with increasing values of time-integrated NDVI after time-integrated NDVI values exceeded about 60.

Top-supported models predicting fecal nitrogen were NDVI ( $p = 0.063$ ), EVI ( $p = 0.062$ ), and an interaction between EVI and tree cover ( $p = 0.038$ ). For all data including both open canopy and forested areas, fecal nitrogen was predicted to increase linearly with increasing NDVI and EVI values. The best supported model predicted that fecal nitrogen decreased with increasing EVI values in open canopy areas but not in forested areas.



**Figure 6.3.** Predicted values of elk nutrition (y-axes) based on top-supported models using remotely-sensed vegetation indices as predictor variables. Plots displaying only one relationship did not include an interaction term with canopy cover. Values of elk nutrition were forage biomass ( $\text{g/m}^2$ ; row 1) herbaceous forage biomass ( $\text{g/m}^2$ ; row 2), digestibility of forage plants (kcal of digestible energy/g of forage; row 3), and elk fecal nitrogen (%; row 4). Remotely-sensed vegetation indices were the Normalized Difference Vegetation Index, a remotely-sensed index of greenness (NDVI); the Enhanced Vegetation Index, an index similar to NDVI that does not saturate at high levels of greenness (EVI); NDVI amplitude, canopy photosynthetic activity throughout the growing season; and time-integrated NDVI, maximum increase in canopy photosynthetic activity during the growing season.

## Discussion

Our results suggest remotely-sensed vegetation indices alone may not serve as an accurate proxy for elk nutrition during summer across landscapes with differing amounts of canopy cover or different land cover types. We found only weak relationships between remotely-sensed vegetation indices and ground-based measurements of elk forage and nutritional intake. The strongest relationship was between herbaceous forage biomass and cubic EVI with a tree cover interaction, suggesting remotely-sensed vegetation indices may capture forage quantity more accurately than they capture forage quality. However, this model only explained 18% of the variability we measured in herbaceous forage biomass, likely due to the high variability in the forage biomass across the sampling sites.

Despite finding only weak relationships between remotely-sensed vegetation indices and ground-based measurements of forage and nutrition, common themes emerged. In gen-

eral, all our measures of elk nutrition tended to increase with increasing remotely-sensed values. We found that accounting for tree cover improved the estimated relationship between remotely-sensed indices and nutrition metrics, highlighting the importance of considering canopy effects when using remotely-sensed indices as a proxy for nutrition. Thus, in areas where greenness varies spatially across the landscape, the addition of land cover type or other covariates may be required to accurately predict elk nutrition using remotely-sensed indices. Open canopy areas were typically predicted to provide higher herbaceous biomass and higher digestibility of forage plants relative to forested areas.

Previous work has shown that remotely-sensed vegetation indices alone can explain as much as 53% of the variation in some measures related to elk nutrition (Garrouette et al. 2016) and can explain as much as 65% of the variation when used in combination with other covariates (Ryan et al. 2012). Studies demonstrating these strong relationships, however, have occurred only in homogeneous open grassland areas. We found substantially lower predictive ability in a heterogeneous landscape where forest canopy cover may mask the true relationships between remotely-sensed vegetation indices and forage conditions in the understory.

Overall, our work emphasizes the importance of interpreting remotely-sensed vegetation indices with caution. While these indices provide valuable ecological and biological insights, their exact relationship with many biologically-relevant measures of nutrition remains undefined. Other work indicates NDVI can map initial green-up of fresh vegetation in open areas, and seasonal migratory movements of ungulates frequently correspond to this fresh “green wave” (Hamel et al. 2009, Bischof et al. 2012). After initial green-up, however, or across areas consisting of a variety of land cover types, the utility of remotely-sensed indices may decrease. Additionally, indices like NDVI appear more predictive of elk nutrition over wider temporal scales of at least the entire season, rather than in discrete snapshots of time throughout a single season (Ryan et al. 2012, Creech et al. 2016, Garrouette et al. 2016). Additional work is needed to more accurately define factors influencing relationships between remotely-sensed vegetation indices and measures of elk nutrition during summer.



## Section 7 — Female and Male Adult Elk Survival

Adult female survival is a key vital rate in ungulate populations (Nelson and Peek 1982, Gaillard et al. 1998, 2000) and can have important effects on population growth rate (Nelson and Peek 1982, Eacker et al. 2016). Adult female survival is generally high and constant in most wild ungulate populations (Gaillard et al. 2000). Reduced adult female survival, whether due to harvest, predation, or other factors, can be the primary driver of declines in ungulate populations (e.g., Owen-Smith and Mason 2005, Hebblewhite and Merrill 2007). Adult male survival has a limited influence on population growth rate but may be associated with changes in conception dates and the synchrony and length of breeding periods (Noyes et al. 1996, 2002). Studies evaluating the effects of altered harvest strategies on males have reported changes to harem size and ratios of bull:cow and calf:cow (Bender 2002, Bender et al. 2002).



Harvest management strategies designed to increase or decrease elk populations often focus on manipulating adult female harvest rates to increase or decrease adult female survival and population growth rate. Harvest management strategies for male elk are generally designed either to maximize hunter opportunity or to restrict hunter opportunity for male elk in efforts to increase male survival and the number of older age-class males (Biederbeck et al. 2001, Bender et al. 2002). Male harvest management is typically not used as a tool for increasing or decreasing population growth rates. Basic knowledge of adult male and female survival can help wildlife managers better assess population responses to management actions and gain insight into factors that may be causing population changes (Biederbeck et al. 2001, Murrow et al. 2009, Hegel et al. 2014). Our goals were to estimate female and male adult survival in the North Sapphire study area during 2014–2016 and to identify cause-specific mortality sources for female and male elk.

### Methods

#### Survival

During February 2014 and 2015, we captured and outfitted elk with remote-upload global positioning system (GPS) collars (Lotek Wireless Inc. model IridiumTrackM 3D and model 3300L, New Market, Ontario, Canada) that triggered a mortality sensor if the collar was stationary for more than 6 hours. Mortality events were remotely detected and transmitted and were investigated as soon as possible. We estimated sex-specific survival rates annually and defined June 1 as the start of the monitoring period based on the biological year, because elk are typically born on or around June 1. Elk entered into the study during a given winter season based on their capture date. Most individuals were monitored for 24 months; however, some individuals were monitored for a shorter period (12 months) because they were captured and collared during the second winter of the project.

We used the Kaplan-Meier (KM) estimator and log-rank tests to provide basic survival estimates and compare survival across monitoring periods (Pollock et al. 1989). The log-rank test is similar to a chi-square test, where the observed and expected numbers of failures are formally compared between groups (i.e., *P*-values of the test estimates). We report 95% confidence intervals (CI) for survival estimates. We compared sex-specific and annual survival with log-rank tests using the R package “survival”. We treated year (2014–2015 and 2015–2016) as a categorical variable in the survival analyses, with each year spanning a “biological” year from June 1 to May 31. We did not consider the effect of age due to the low variation in ages captured, with the majority of elk falling into the prime (2–9 year old) age category (Raithel et al. 2007).

### Cause-specific mortality

We determined the cause and timing of mortality based on factors such as presence of carnivore tracks and scat, location and types of wounds to the animal (location, depth and size of bite and claw marks), signs of struggle, severity and timing of injuries (pre- or post-mortem based on subcutaneous hemorrhaging), patterns of consumption, presence and patterns of carcass caching, and signs of scavenging (Smith and Anderson 1996, Barber-Meyer et al. 2008). We also documented photographic evidence at each mortality location. We categorized mortality sources for adult female elk as mountain lion, wolf, unknown, natural, (e.g., non-predation starvation or disease), and human-related (e.g., hunter harvest, vehicle collision, or fence entanglement). We only classified a mortality event to a specific cause if the confidence level was certain, which meant that evidence was sufficiently clear and unambiguous as to the source of mortality.

## **Results**

### Survival

In 2014, we deployed 45 collars on female elk and 20 collars on male elk. In 2015, we deployed 3 collars on female elk and 8 collars on male elk. During 2014–2015, we observed 6 female and 9 male elk mortality events. During 2015–2016, we observed 1 female and 6 male elk mortality events. We removed mortalities of unknown mortality date (2 male elk; see *Cause-specific mortality* below) and individuals of unknown fate (5 female and 7 male elk) from the analysis. This resulted in a total of 43 female elk and 19 male elk included in our survival analysis, totaling 81 female and 30 male elk-years. During 2014–2015, 40 collared female elk entered the monitoring period and 5 female elk mortalities occurred, and during 2015–2016, 38 collared female elk entered the monitoring period and 2 female elk mortalities occurred. During 2014–2015, 13 collared male elk entered the monitoring period and 8 male elk mortalities occurred, and during 2015–2016, 11 collared male elk entered the monitoring period and 5 male elk mortalities occurred.

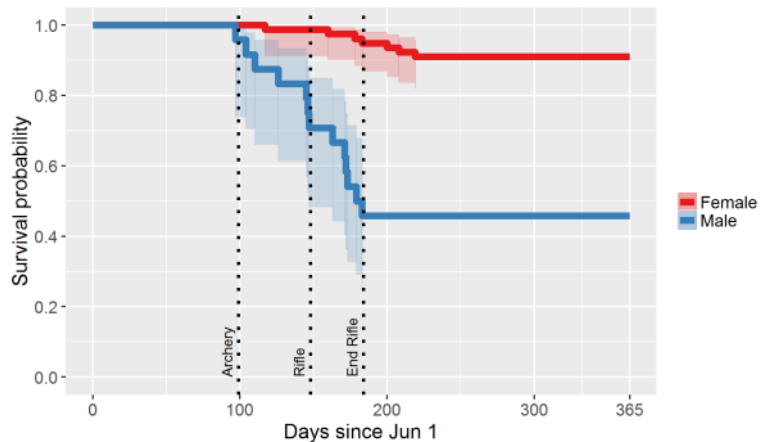
Annual survival rates were significantly different between sexes (Figure 7.1; log-rank test = 31.25 on 1 d.f.,  $p < 0.001$ ). The annual survival rate for adult female elk was 0.91 (95% confidence interval [CI] = 0.82–0.96) and for adult male elk was 0.46 (95% CI = 0.26–0.64). Annual adult female survival was higher in 2015–2016 at 0.95 (95% CI = 0.81–0.99) than in 2014–

2015 at 0.88 (95% CI = 0.73–0.95), but there was no evidence of a significant difference between years (Figure 7.2; log-rank test = 1.28 on 1 d.f.,  $p = 0.26$ ). Similar to patterns in adult female survival, annual adult male survival was higher in 2015–2016 at 0.55 (95% CI 0.23–0.78) than in 2014–2015 at 0.39 (95% CI 0.14–0.63), but there was no evidence of a significant difference between years (Figure 7.3; log-rank test = 0.93 on 1 d.f.,  $p = 0.33$ ).

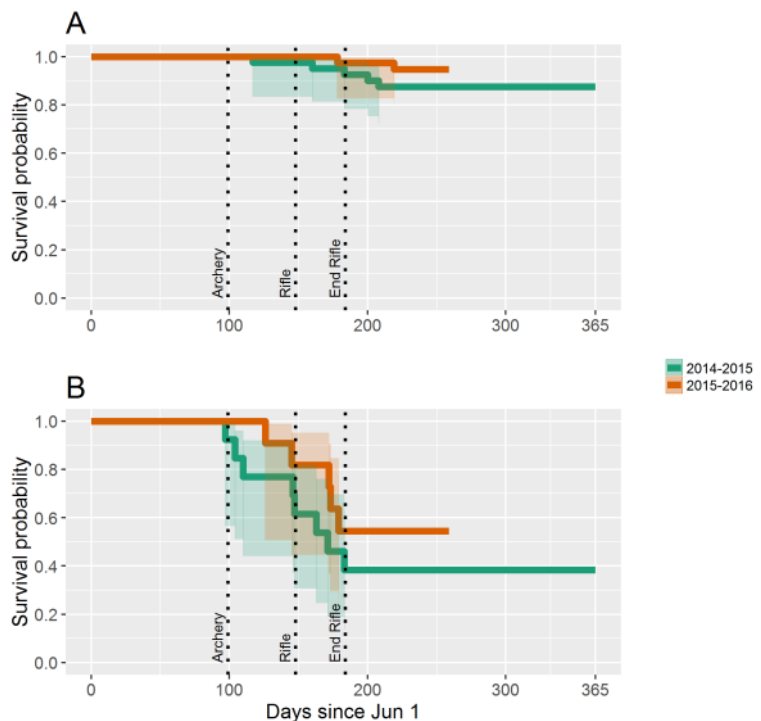
Annual survival rates may be biased high for two reasons: hunter avoidance of harvesting colored animals and survival of the same individuals across years. Annual survival estimates including the same individuals that survived year 1 in the second year and individuals surviving the first year may be more likely to also survive the second year. Using data collected from only the first year of monitoring each individual, the annual survival rate was 0.88 (95% CI = 0.73–0.95) for adult female elk and 0.39 (95% CI = 0.14–0.63) for adult male elk.

#### Cause-specific mortality

We investigated 7 female and 15 male elk mortalities (Figure 7.4). Six female mortalities were human-related, including 2 late-season damage harvests, 1 rifle season harvest, 1 illegal harvest, 1 archery season wounding loss, and 1 vehicle collision. The remaining female mortality was of unknown cause. Of the harvest-related mortalities for females, all occurred on



**Figure 7.1.** Kaplan-Meier survival curves and 95% confidence intervals (shaded bands) for female (green) and male (orange) elk. Survival estimates are based on the periods June 1–May 31 for 2014–2015 and 2015–2016. Dotted vertical lines represent relevant days of archery and rifle general hunting seasons.



**Figure 7.2.** Kaplan-Meier survival curves and 95% confidence intervals by year for female (panel A) and male (panel B) elk. Survival estimates based on the periods June 1–May 31 for 2014–2015 (green) and 2015–2016 (orange). Dotted vertical lines represent relevant days of archery and rifle hunting seasons.

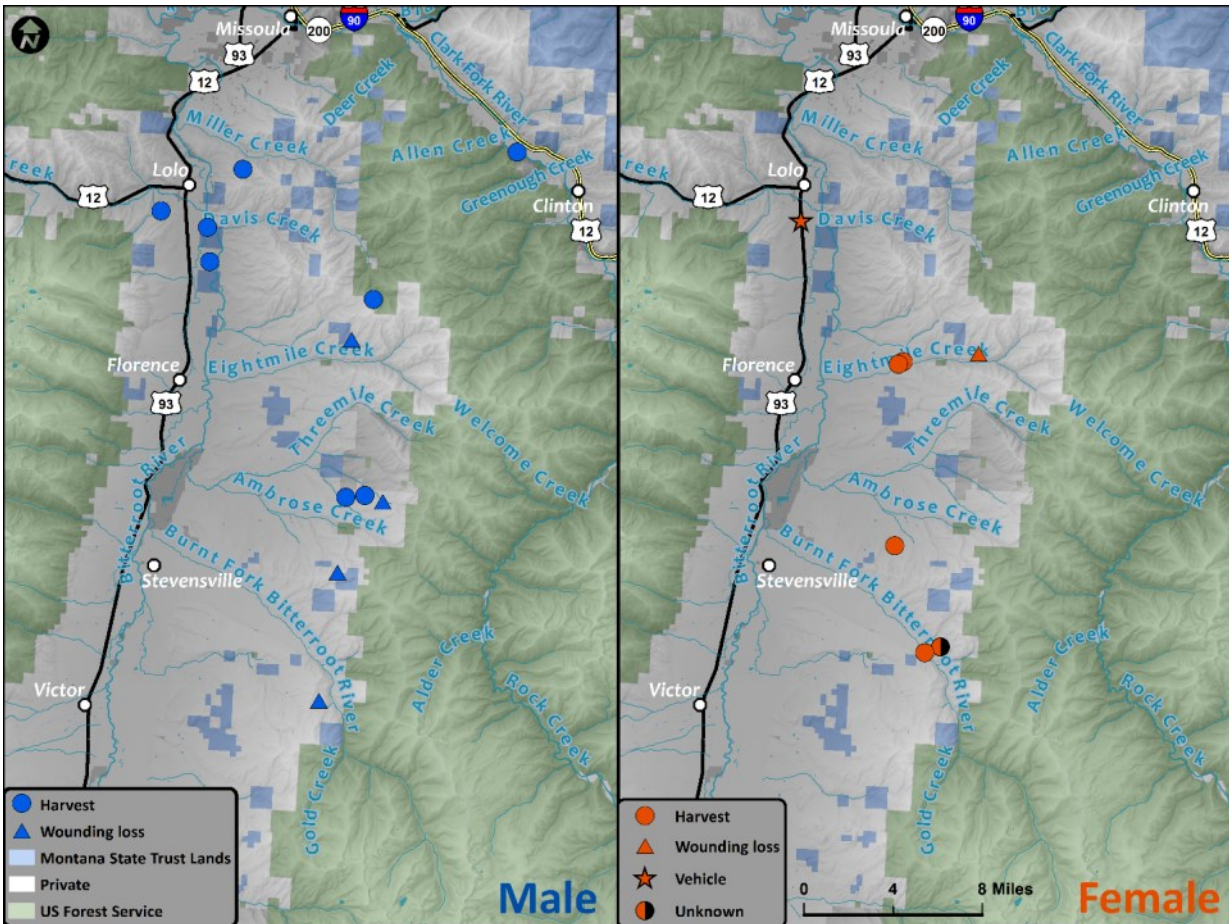


Figure 7.4. Locations and cause of adult male (blue) and female (orange) elk mortality in the North Sapphire elk population during 2014 – 2016. Three male mortality locations not shown due to missing location data (1 harvested on private property near Stevensville, 1 cut collar found in Miller Creek, and 1 cut collar found in Slocum Creek-Burnt Fork).

private properties. Thirteen adult male mortalities were human-related, including 7 rifle season harvests, 3 rifle season wounding losses, 2 archery season harvests, and 1 archery season wounding loss. The remaining 2 adult male mortalities were of unknown cause, date, and location, however, the collars were found cut suggesting illegal harvest. Of the 13 male mortalities known to be harvest-related, 5 occurred on private, 6 occurred on public, and 2 likely occurred on public, but exact mortality location was unknown.

## Discussion

Effectively managing harvested ungulate populations requires an understanding of factors affecting adult survival rates. Harvest of adult females can be an effective means of increasing or decreasing population growth rates to meet management objectives. Recent efforts to increase female harvest and reduce survival rate through damage hunts have been implemented to reduce the North Sapphire elk population, however, the population has remained above objective (Section 2). Here, we found that adult female survival was estimated to be high ( $\bar{x} = 0.91$ ) and constant among years (2014-2015) as expected (Gaillard et al. 2000), and was not



different from the average adult female survival rate reported for other harvested and unharvested populations across western North America which ranged from 0.84–0.94 (Brodie et al. 2013). The primary source of female mortality was human-related (85.6%), including primarily harvest but also 1 vehicle collision. In most hunted elk populations, the major cause of mortality is commonly harvest-related (Raedeke et al. 2002, Brodie et al. 2013), as is the case in this population. At the current mountain lion and wolf population densities, predation was not an important factor in limiting elk population growth rate. We expected some level of predator-caused mortalities given the presence of both wolves and mountain lions in the area; however, we observed no mortalities associated with predation during this 2-year study. One mortality was recorded as a possible mountain lion predation, but there was no evidence to determine whether the elk was killed or scavenged post-mortality by the lion.

While the majority of mortalities were associated with harvest, the high survival rates of females combined with the low estimated annual harvest of antlerless elk (Section 2) suggest that female harvest is not occurring at sufficient levels to reduce the overall population. Management action to reduce population size likely requires increased harvest of adult female elk; however, elk use of private properties (Section 8) with limited public hunting access may restrict the ability of managers to manipulate harvest numbers during the general hunting season. Developing strategies to increase harvest on these private properties or redistribute elk onto public lands may be effective to meet population objectives. However, harvest management on private lands varies across the study area with some landowners seeking to protect elk from harvest and others seeking to increase harvest and redistribute elk back to public lands.

Adult male elk survival ( $\bar{x} = 0.46$ ) was estimated to be significantly lower than female elk survival ( $\bar{x} = 0.91$ ) with no statistical evidence of variability between years; however, sample size was low. Adult male elk survival was estimated to be within the range of typical annual survival rates found by several studies in male-harvested populations in Montana (DeSimone et al. 1996, Hamlin and Ross 2002), Idaho (Unsworth et al. 1993), Wyoming (Smith and Anderson 1998), Utah (Kimball and Wolfe 1974), and Oregon (Biederbeck et al. 2001). Annual survival rates of adult males in the Elkhorn (1984-1991) and Gravelly-Snowcrest (1990-1998) populations of Montana averaged 0.47 (range 0.05-0.76%) and 0.25 (range 0.08-0.46), respectively (DeSimone et al. 1996, Hamlin and Ross 2002). Human-related harvest in these populations accounted for 96.8 and 91.2% of mortalities, respectively. Reported survival rates for other harvested populations outside Montana ranged from 0.45-0.60, with hunter harvest accounting for 86-90% of male elk mortalities (Kimball and Wolfe 1974, Unsworth et al. 1993, Smith and Anderson 1998, Biederbeck et al. 2001, Raedeke et al. 2002). Hunting-related mortality (harvest and wounding loss) in this study accounted for at least 86.7%. We recorded no mortalities associated with predation or natural causes, which accounted for 3.2% and 0% in the Elkhorn and Gravelly-Snowcrest populations, respectively. Approximately 50% of harvest mortalities in the current study occurred on public lands, indicating more public hunter opportunity for male than for female elk (0%) in this population. Given the adult male elk survival rate, adequate recruitment rate (Section 2), and recent observed bull: adult female ratios (Section 2), current levels of adult male harvest mortality are likely sustainable given current hunter opportunity in this population.



## Section 8 — Elk Distribution and Movement Patterns

### Introduction

The North Sapphire elk occupy a diverse and heterogeneous landscape that includes a matrix of public and private land with varying vegetation cover types, land uses, and hunter access opportunities. Seasonal patterns of habitat use by the North Sapphire elk are likely strongly influenced by this landscape mosaic offering variable habitat and forage quality and variable risks associated with human harvest. Response of elk to this variable landscape may have survival and reproductive consequences as elk seek to minimize mortality risks and maximize forage opportunities. During fall hunting seasons, elk may seek refuge from harvest risk by increasing use of private properties that limit or restrict hunter access. Increased use of private lands by big game species is a growing challenge in wildlife management because wildlife managers lose an important tool in managing populations at objective levels if private landowners do not allow hunting (Haggerty and Travis 2006). A better understanding of seasonal elk distributions and movement behaviors is important as wildlife managers strive to balance concerns of private landowners and hunters regarding elk distributions and manage elk within population objective levels.

We collected elk location information from female and male elk to 1) describe annual and seasonal ranges (calving, summer, fall, and winter/spring) of female and male elk; 2) evaluate general movement patterns, including understanding the amount of public/private land use throughout the year, and 3) identify potential travel corridors and road crossings. The delineation and description of elk seasonal ranges and movement patterns is useful to ensure that elk habitat and population management goals are directed to areas currently used by elk, as well as estimating the availability of elk on public lands during the hunting season. Identifying potential travel corridors and road crossings may be useful for maintaining and conserving landscape connectivity, as well as for transportation planning. In Section 9, we provide an in-depth evaluation of the variable migratory behavior strategies of elk and the consequences of these strategies. In Section 10, we provide an in-depth evaluation of the relative effects of the fall hunting season on female and male elk habitat selection and potential trade-offs of forage and mortality risk.

### Methods

#### Elk collaring and monitoring

We deployed 60 remote-upload global positioning system (GPS) collars (Lotek Wireless Inc. model IridiumTrackM 3D, New Market, Ontario, Canada) to collect location data from female and male elk. We also deployed 5 store-on board global positioning system (GPS) collars (Lotek Wireless Inc. model 3300L, New



Market, Ontario, Canada). We programmed all collars to record 24 locations per day. In 2014, we deployed 45 collars on female elk and 20 collars on male elk. We retrieved 11 functional collars from 2014 mortalities, and redeployed these 11 collars on 3 female and 8 male elk in 2015. We fit each collar with a timed drop-off mechanism set to release after 104 weeks, at which time we retrieved the collars and downloaded the data from store-on board collars.

### Annual and seasonal distributions

To delineate seasonal and annual distributions for female and male elk, we randomly sampled 5 locations per day per collared elk and used a 95% kernel density estimator. The 95% kernel density distribution is the area in which the probability of finding an animal is equal to 0.95. We partitioned the calendar year into 5 seasons: calving, summer, archery hunting season, rifle hunting season, and winter-spring. We defined calving as 20 May–15 June, summer as 1 July until 1 week prior to the opening of archery season, and winter-spring as 1 week after the close of rifle season through 1 May. We defined archery and rifle seasons according to the annual Montana general elk archery and rifle season dates, where the 6-week archery season starts on the 1<sup>st</sup> Saturday in September and the 5-week rifle season starts 5 weeks prior to the Saturday after Thanksgiving. Annual distributions were defined as spanning from calving to the end of winter-spring. We calculated and summarized annual distributions by sex for each year. We extracted land ownership, public hunter accessibility, and vegetation cover type for each annual and seasonal distribution to assess land and vegetation cover use. Land ownership categories included private, state, and federal. We classified hunter access into 2 categories: accessible to public hunting and restricted public hunting access. Areas accessible to public hunting included publicly-owned state and federal lands that allowed hunting and private properties enrolled in MFWP's Block Management program, such as The Nature Conservancy and Weyerhaeuser Company (formerly Plum Creek Timber Company). Areas of restricted public hunting access included private lands that allowed for hunting without a fee to only family and friends or through any other system that restricted free, unlimited public access. Vegetation cover types included dry forests (primarily *Pseudotsuga menziesii* and *Pinus ponderosa*), mesic forests (primarily *Picea engelmannii*, *Abies lasiocarpa*, *Abies grandis*, *Tsuga heterophylla*, and *Thuja plicata*), open grassland/shrubland, montane riparian, valley bottom riparian, irrigated agricultural areas, and dry agricultural areas. Additionally, within each annual and seasonal range, we identified and described core use areas (i.e., areas estimated from kernel density methods to have higher relative densities of locations).

### Corridors & road crossings

We identified potential travel corridors of elk by first creating line segments between consecutive GPS locations for each individual across all years, filtering the line segments to include only fixes that were 2 hours apart and greater than 2,500 m in length, and mapping the density of resulting line segments. The line segments represent quick, long-distance, and directional movements that typify the definition of animal-defined corridors (LaPoint et al. 2013). Localized regions with repetitive movements completed by the same or multiple animals over the duration of the study are represented by higher densities and can be interpreted as potentially important areas for travel by elk. Finally, we identified the location and timing of all road

crossings of US Highway 93 recording by GPS locations to isolate highway regions frequently used by elk.

## Results

We obtained 453,225 GPS location fixes from 76 individual elk (48 females, 28 males) spanning from 26 February 2014 to 16 February 2016. We collected 374–8,860 locations ranging from 30–720 days per individual elk. Elevations of female elk locations ranged from 955–2,657 m and averaged 1,368 m, and of male elk ranged from 963–2,675 m and averaged 1,640 m. Slope of female elk locations ranged from 0–51° and averaged 13°, and of male elk locations ranged from 0–48° and averaged 17°. Canopy cover of female elk locations ranged from 0–95% and averaged 14%, and for male elk locations ranged from 0–75% and averaged 24%. Seventy-five percent of female elk locations occurred on private land, 18% on federal, and 7% on state. Forty-eight percent of male elk locations occurred on private land, 41% on federal, and 11% on state. Thirty-one percent of female elk locations and 67% of male elk locations occurred on areas accessible to public hunting. Of the locations for female elk, 45% occurred in open grassland/shrubland/woodland, 32% in forest, 7% in irrigated agricultural, 5% in dry agricultural, 4% in valley bottom riparian, 4% in burned forest, and 3% in montane riparian areas. Of the locations for male elk, 44% occurred in forest, 28% in open grassland/shrubland/woodland, 18% in burned forest, 6% in montane riparian, 2% in dry agricultural, 1% in irrigated agricultural, and 1% in valley bottom riparian areas.



### Annual and seasonal distributions.

We used 189,456 GPS locations to delineate seasonal distributions after constraining locations to our defined seasons, sampling 5 locations per animal per day, and removing 524 locations with high values of dilution of precision ( $> 10$ ), a measurement of horizontal error from imprecision of satellite acquisitions. Individual elk demonstrated a large amount of variation in size and composition of annual distributions (Table 8.1). Individual female annual ranges in 2014 ranged in size from 30–172 km<sup>2</sup> and averaged  $92 \pm 35$  km<sup>2</sup> ( $\pm$  SD) and in 2015 ranged from 27–150 km<sup>2</sup> and averaged  $84 \pm 29$  km<sup>2</sup>. Individual male annual ranges in 2014 ranged from

**Table 8.1. Mean, standard deviation (SD), minimum, and maximum area (km<sup>2</sup>) of estimated individual annual ranges (95% kernel density) and number of individual by sex and year for the North Sapphire elk population.**

Year	Female					Male				
	Mean (km <sup>2</sup> )	SD	Min	Max	No. Elk	Mean (km <sup>2</sup> )	SD	Min	Max	No. Elk
2014	92.6	35	29.9	172	42	118.4	76.9	24.4	310.4	19
2015	84	29.2	27.3	150	40	94.4	50.3	25.3	197.3	14

24–310 km<sup>2</sup> and averaged  $109 \pm 71$  km<sup>2</sup> and in 2015 ranged from 25–197 km<sup>2</sup> and averaged  $94 \pm 50$  km<sup>2</sup>. Individual male annual range size averages may be biased low due to higher mortality rates.

Population annual ranges varied by sex, with male ranges 10–30% larger in area than female ranges (Table 8.2; Figure 8.1). Female core use areas (i.e., areas of highest density of locations) within the annual range generally occurred at lower elevations than males and were primarily located between north of Miller Creek and Eightmile Creek, between Ambrose Creek and Burnt Fork, and in the Greenough/Allen Creek area. Land ownership within the female annual range was primarily private (60.6–62.7%), with federal and state lands comprising 30.5–32.9 and 6.2–6.7%, respectively (Panel A, Figure 8.2). Approximately half (49.5–50.2%) of the female annual range consisted of areas accessible to public hunting (Panel B, Figure 8.2). Dry forest (35.8–36.4%) and grassland/shrubland (34.9–35.0%) accounted for the majority of vegetation types within the female annual range (Panel C, Figure 8.2). Mesic forests comprised 10.5–11.4% and lower elevation cover types including valley bottom riparian, irrigated agricultural, and dry agricultural areas comprised approximately 3.6%, 3.6%, and 3.1%, respectively.

Male core use areas within the annual range were primarily located between Miller Creek and Eightmile Creek, between Threemile Creek and Ambrose Creek, in the Welcome Creek region, and along Burnt Fork. Land ownership within the male annual range was primarily federal (50.6–51.9%) and private (40.6–42.5%; Figure 8.2), with state lands comprising 6.9–7.5%. The majority (68.9–69.7%) of the male annual range consisted of areas accessible to public hunting. Dry forest (34.8–37.8%), grassland/shrubland (28.1–29.7%), and mesic forest (19.7–23.8%) accounted for the majority of vegetation types within the male annual range. Lower-elevation cover types including valley bottom riparian, irrigated agricultural, and dry agricultural areas comprised approximately 2.1%, 1.4%, and 2.5%, respectively.

Population seasonal ranges varied by sex and year, with males generally using higher-elevation areas than females (Table 8.3; Figure 8.3–8.5). For females, calving range was the largest in area of all seasonal ranges, representing wide dispersion of individuals across the landscape. Calving seasonal ranges for females occurred primarily on private lands (Figure 8.6), with core use areas occurring in 4 general regions, including south of Lolo along the Bitterroot River, the middle reaches of Eightmile Creek, the middle reaches of Burnt Fork, and Deer Creek southeast of Missoula. These core use areas were mostly on private lands with scattered blocks of state land, with the exception of the Deer Creek area occurring primarily on federal lands. The core use area south of Lolo provides protected valley bottom riparian forests along the Bitterroot River adjacent to agricultural areas and grassland foothill benches. The remaining core use areas were located in rolling foothills adjacent to or in timbered slopes. During the calving season, males were generally at higher elevations in foothill grassland/shrubland and forest vegetation cover types (Figure 8.7), with little to no use of valley bottom riparian and ag-

**Table 8.2. Area (km<sup>2</sup>) of and number of elk used in estimated population annual ranges (95% kernel density) by sex and year for the North Sapphire elk population. Elk captured in winter 2015 were included in calculation of 2014 annual range due to definition of year (i.e., biological year spanning 20 May–1 May).**

Year	Female		Male	
	Area (km <sup>2</sup> )	No. Elk	Area (km <sup>2</sup> )	No. Elk
2014	750.1	45	974.9	27
2015	830.4	40	911.5	15



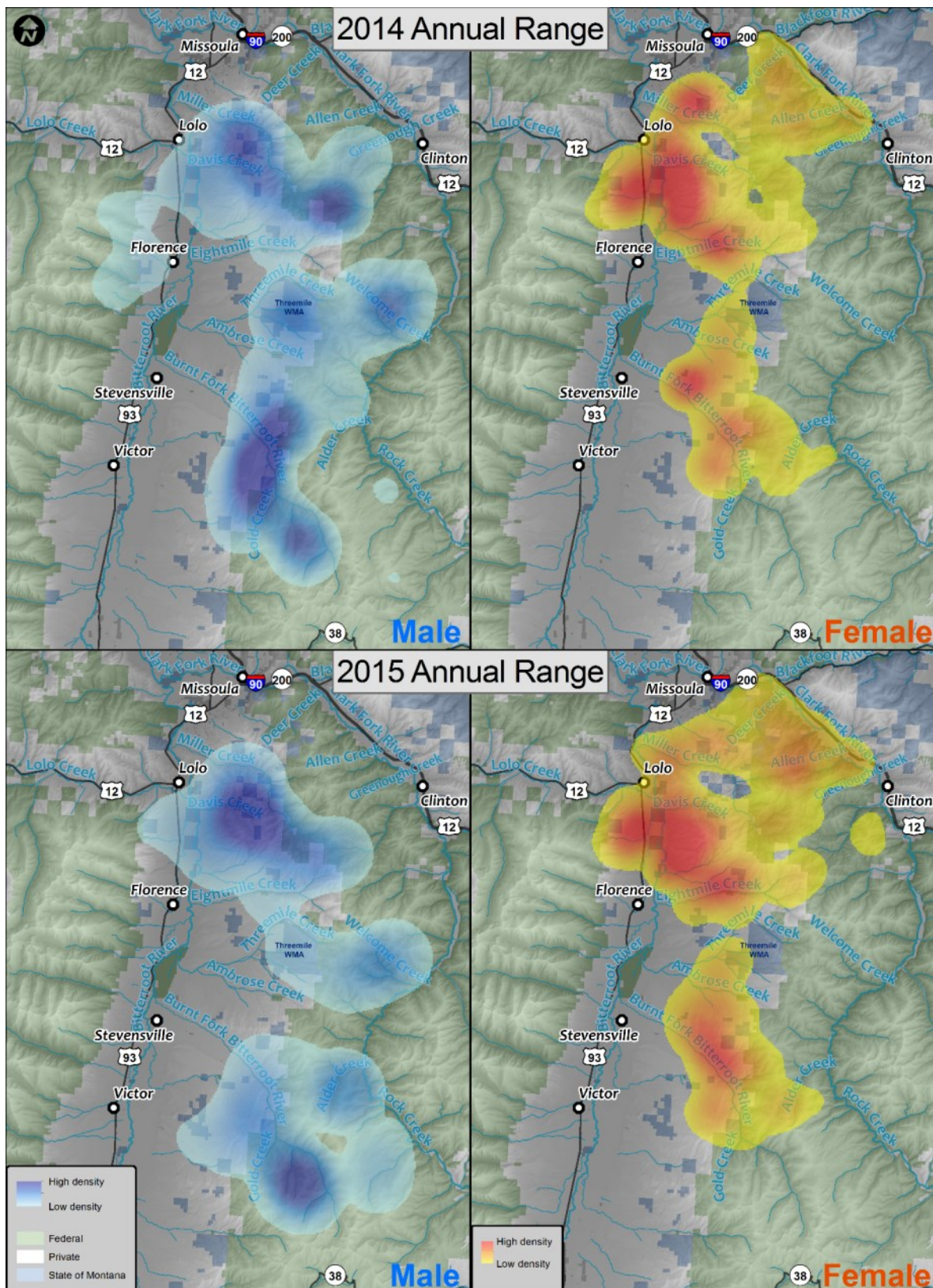
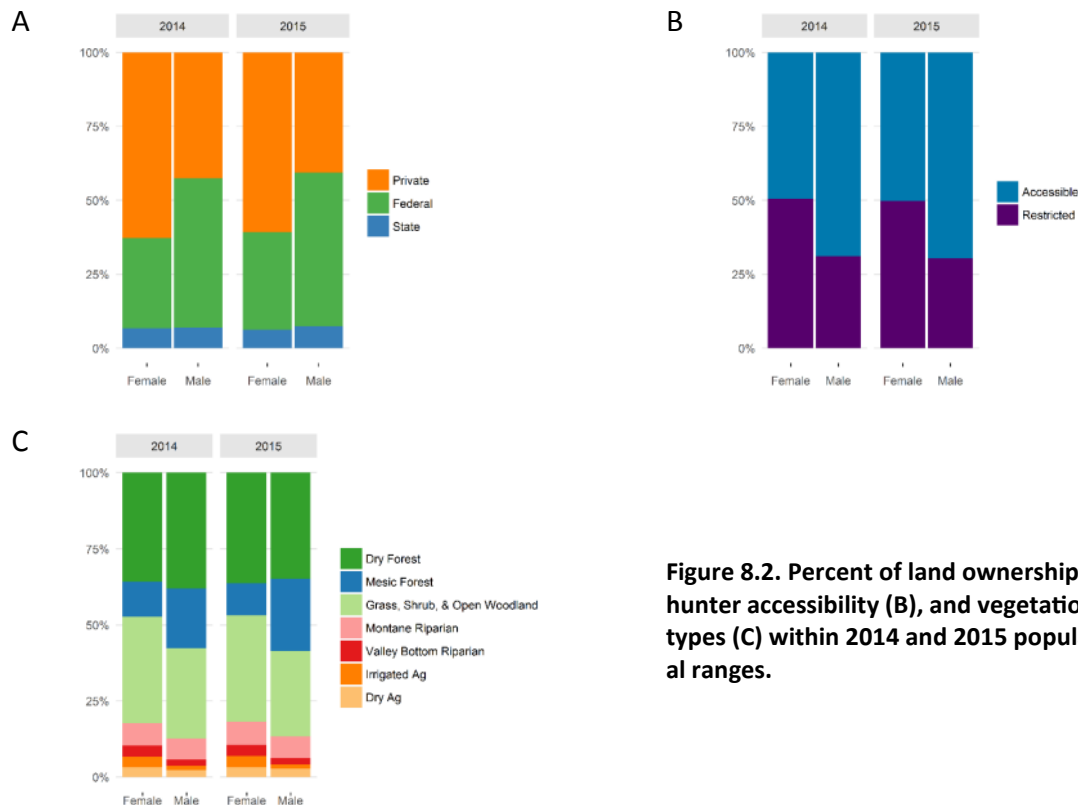


Figure 8.1. Annual ranges of male and female elk for 2014 and 2015 in the North Sapphire elk population. Darker regions within annual ranges indicate higher density of elk GPS locations.





**Figure 8.2. Percent of land ownership (A), public hunter accessibility (B), and vegetation cover types (C) within 2014 and 2015 population annual ranges.**

gricultural areas. Male core use areas included the Miller Creek drainage, between the upper reaches of Threemile Creek and Ambrose Creek, the upper reaches of Welcome Creek, and the upper reaches of Burnt Fork. In 2015, a core use area in Alder Creek was identified.

During summer, both male and female elk generally shifted to higher-elevation forested areas as compared to the calving season; however, a portion of female elk remained resident at lower elevations south of Lolo, primarily on grassland/shrubland foothills and private agricultural lands (Figure 8.3). Use of private agricultural and grassland/shrubland properties was lowest, and use of federal forested land was higher, during the summer season for both sexes as compared to all other seasons (Figure 8.6 and 8.7). The middle reaches of Eightmile Creek remained a core use area for females. The female core use area along Burnt Fork shifted to the higher elevation terrain along the crest of the Sapphire Mountains, and the female core use area in the Deer Creek area shifted south and east to higher elevations at the upper reaches of Allen Creek.

The shift in distributions between summer and archery hunting seasons differed for female and male elk (Figure 8.3 and 8.4), as expected given the onset of the hunting and breeding seasons. Female distributions during the archery season contracted marginally in total area compared to the summer season but had relatively similar mean elevations and compositions of land ownership, hunter accessibility, and vegetation cover type. During the archery season, female elk appeared to congregate primarily in the region south of Lolo extending to the middle reaches of Eightmile Creek, but core use areas were also identified along the middle reaches of Burnt Fork and between Deer Creek and Allen Creek. Male distributions during archery seasons

**Table 8.3. Area (km<sup>2</sup>) of and number of elk used in estimated seasonal ranges (95% kernel density) by sex and year.**

Year	Season	Female			Male		
		Area (km <sup>2</sup> )	Mean Elev. (m)	No. Elk	Area (km <sup>2</sup> )	Mean Elev. (m)	No. Elk
2013	Winter-Spring	432.8	1268	43	406.9	1462	20
2014	Calving	872.7	1437	42	1038.7	1622	19
	Summer	788.5	1510	42	853.5	1721	19
	Archery	754.5	1500	42	1090.1	1625	18
	Rifle	523.8	1350	41	951.9	1589	13
	Winter-Spring	438.8	1276	42	467.7	1492	15
2015	Calving	886.4	1457	40	844.9	1747	15
	Summer	789.9	1505	40	703.0	1789	14
	Archery	688.2	1416	39	1022.7	1594	13
	Rifle	693.3	1365	38	657.6	1576	8
	Winter-Spring	623.6	1306	36	242.5*	1451	4

\* The limited winter-spring distribution in 2015 was due to there being only 4 GPS collars represented in the population at that time due to high mortality rates of males during the hunting seasons.

shifted considerably as compared to summer distributions, with mean elevations about 100–200 m lower and ranges composed of a greater proportion of private properties, areas restricting hunter access, and lower-elevation vegetation types (valley bottom riparian, grassland/shrubland, and agricultural areas; Figure 8.6, 8.7, and 8.8). The total area of male distribution during archery seasons for both years was highest compared to other seasons (Table 8.3), representing a high degree of movement and dispersion during this time. We identified 5 male core use areas during the 2014 season, including south of Lolo along the Bitterroot River, the headwaters of Miller Creek, the headwaters of Welcome Creek, between Ambrose Creek and Burnt Fork, and west of the confluence of Burnt Fork and Gold Creek. During the 2015 season, core use areas were primarily south of Lolo along the Bitterroot River, along the crest of the Sapphire Mountains between Threemile Creek and Ambrose Creek, and south of the middle reaches of Burnt Fork.

Distributions during rifle season for female and male elk (Figure 8.4) had lower mean elevations and consisted of greater proportions of private properties, areas restricting hunter access, and lower-elevation vegetation types (valley bottom riparian and agricultural areas; Figure 8.6, 8.7, and 8.8) as compared to the archery seasons. Female core use areas during the rifle hunting season were located primarily between the lower reaches of Miller Creek to Eightmile Creek and between the middle reaches of Ambrose Creek and Burnt Fork. Male core use areas overlapped strongly with females and were primarily located between Miller Creek and Eightmile Creek and around the middle reaches of Burnt Fork. Core use areas for males during this season also occurred in the region of the Threemile Wildlife Management Area and the upper reaches of Burnt Fork.

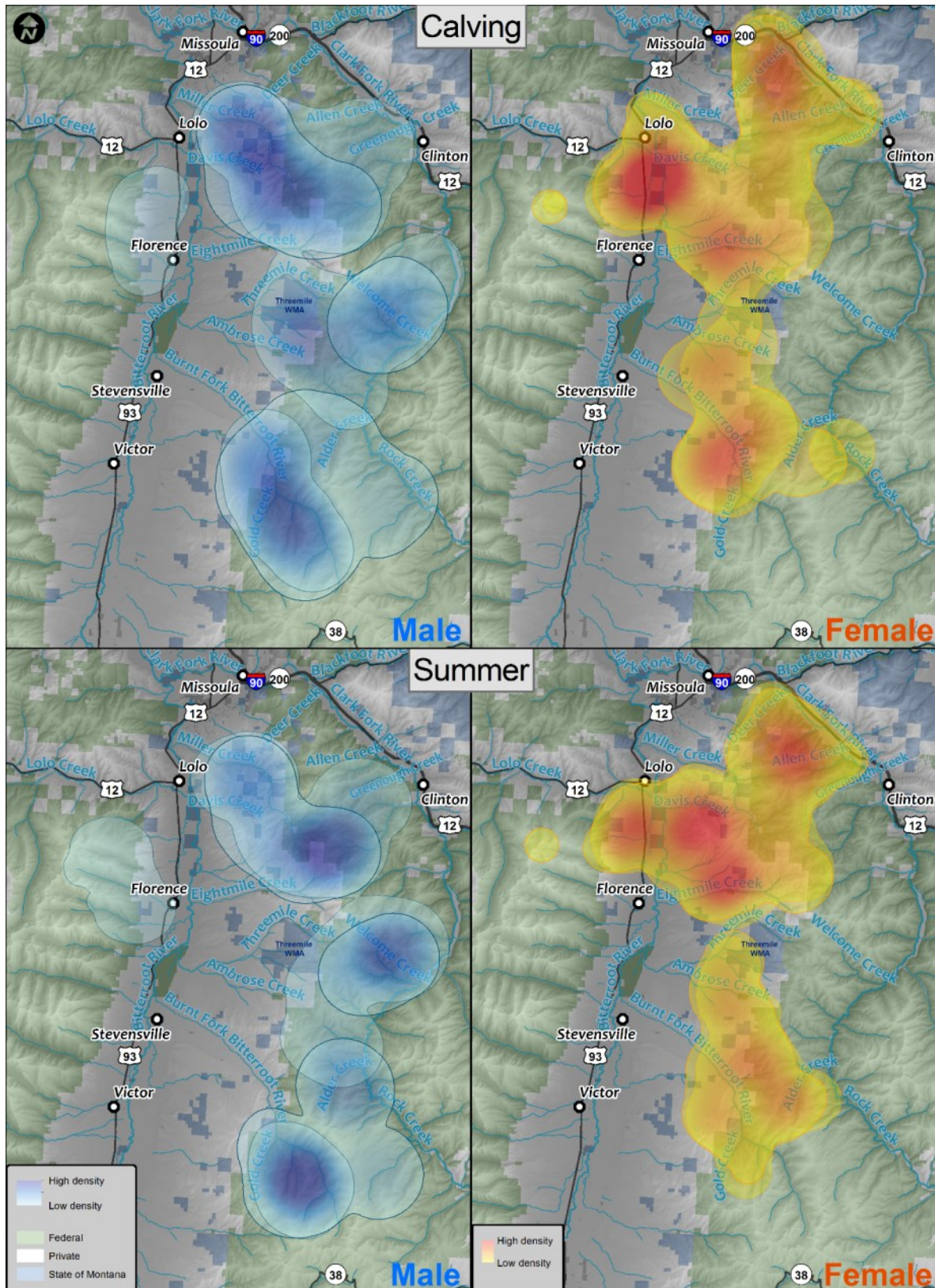


Figure 8.3. Calving and summer distributions for male and female elk showing the relative density of locations for GPS-collared elk (2015 distributions overlaid on top of 2014).



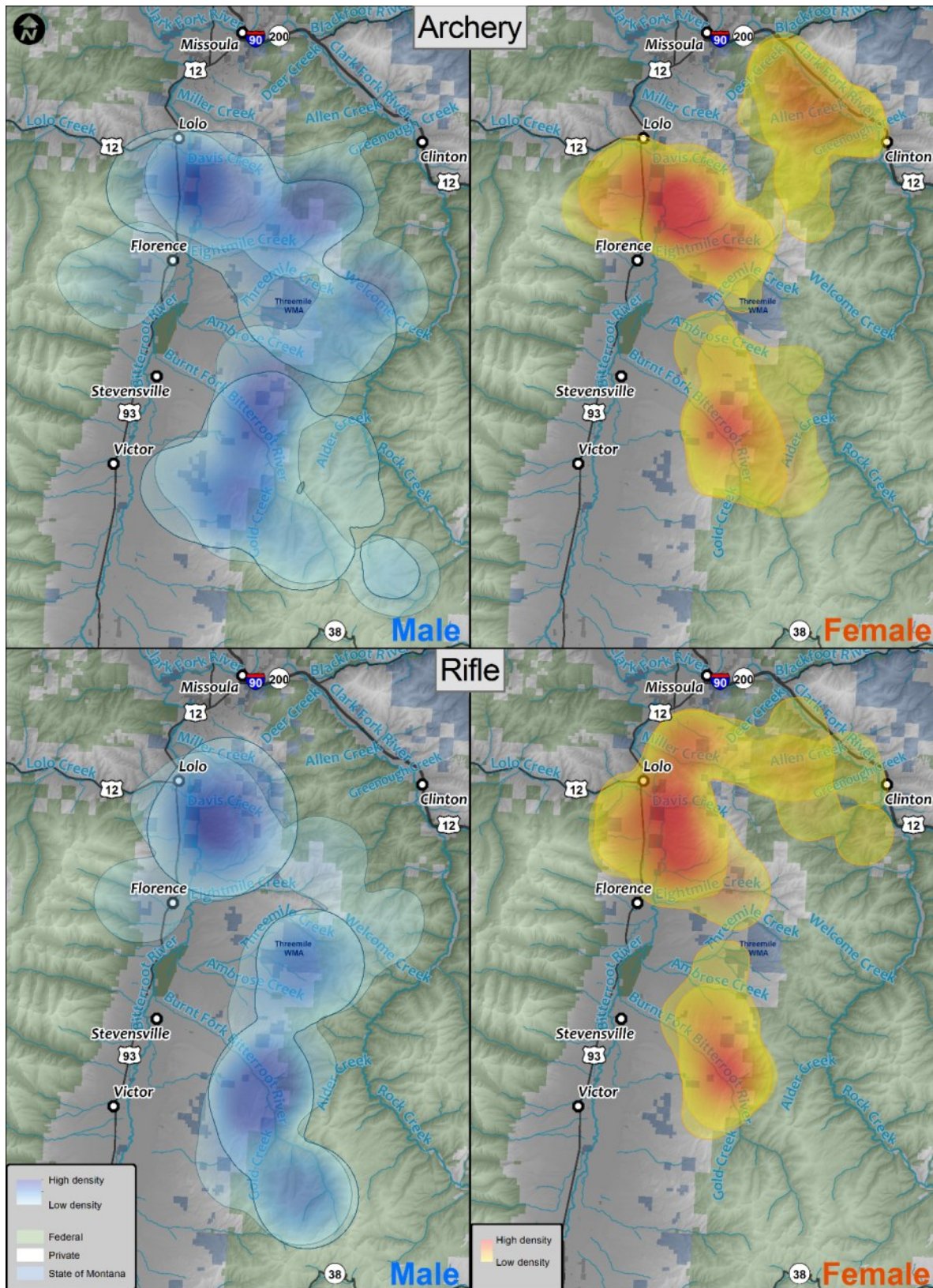
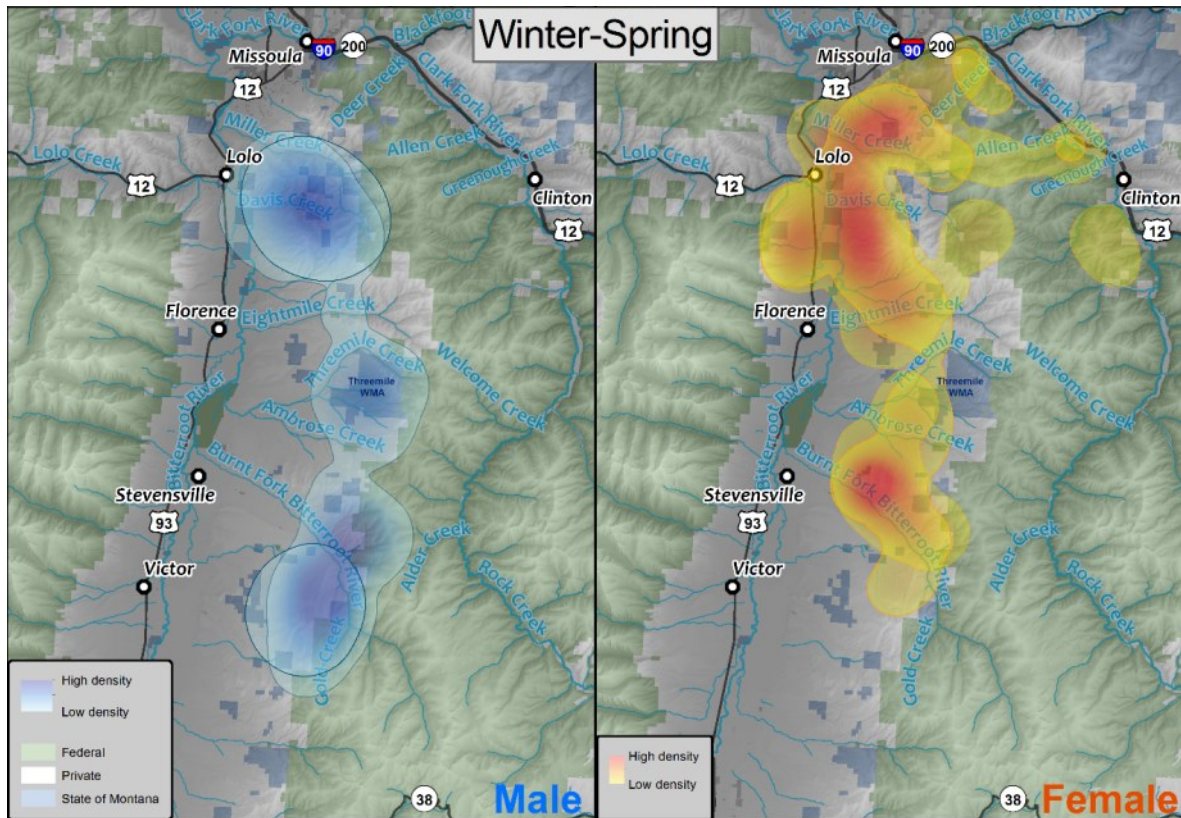


Figure 8.4. Archery and rifle distributions for male and female elk showing the relative density of locations for GPS-collared elk (2015 distributions overlaid on top of 2014).





**Figure 8.5.** Winter-spring distributions for male and female elk showing the relative density of locations for GPS-collared elk (2015 distributions overlaid on top of 2014).

Winter-spring distributions (Figure 8.5) had the smallest areas, occurred at the lowest mean elevations, and were comprised of the greatest proportion of privately owned properties as compared to all other seasonal distributions (Table 8.3; Figure 8.6). Winter-spring distributions also had proportionally the lowest amount of forest and highest amount of grassland/shrubland cover types (Figure 8.7). Female elk occupied areas approximately 150–220 m lower in mean elevation and with a proportionally higher amount of valley bottom riparian and irrigated agricultural areas than males. Female core use areas occurred in three primary regions, including the lower Miller Creek drainage, south of Lolo along the Bitterroot River to Eightmile Creek, and between Ambrose Creek and the lower reaches of Burnt Fork. Male core use areas occurred in three primary regions, including the upper Davis Creek south of Miller Creek, the Threemile Wildlife Management Refuge, and the middle reaches of Burnt Fork.

### Corridors & road crossings

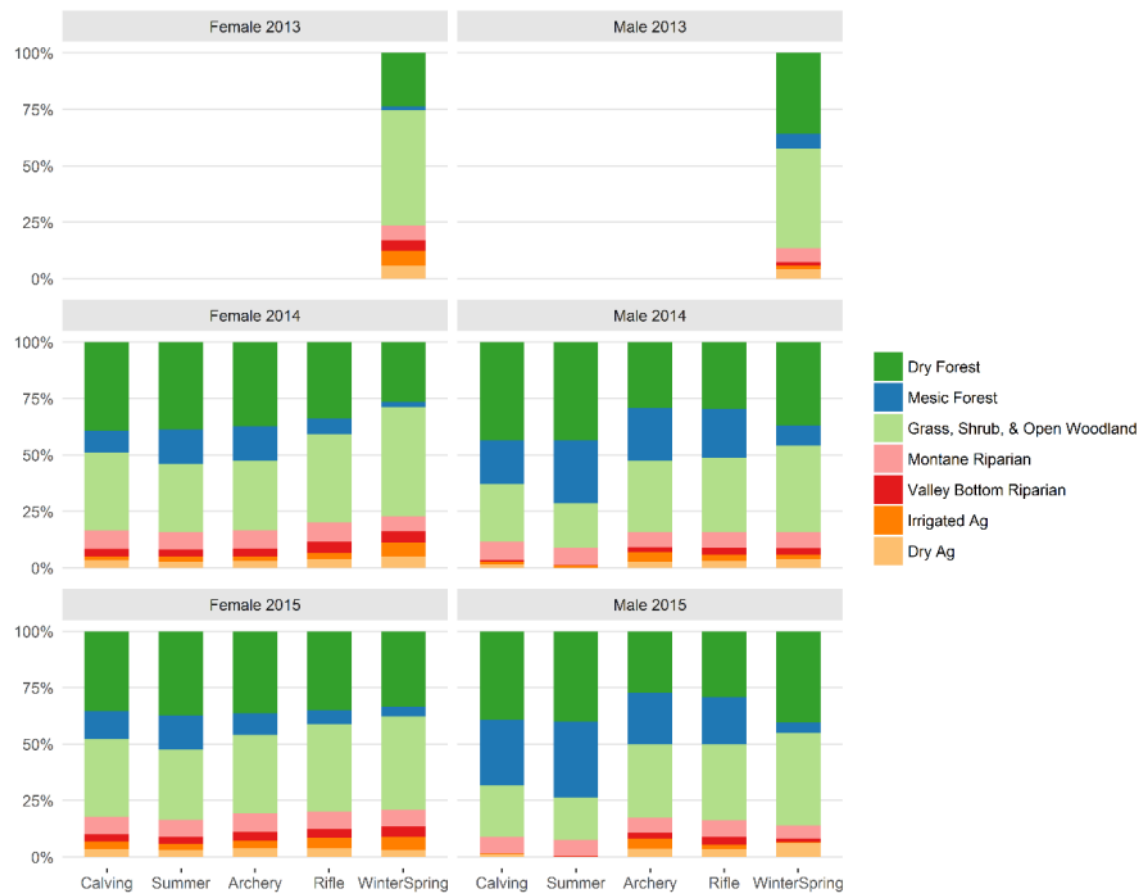
We identified several localized regions that may be important travel corridors based on our definition of “corridor” (Figure 8.9). Other travel corridors likely exist but were not represented in our sample of GPS-collared individuals or were outside our definition (e.g., slow, directional movements toward summer range). Additionally, the identified corridors may reflect increased movement rates due to increased mortality risks during hunting seasons or due to predators. Here, we describe 5 of the most prominent travel corridors (as indicated in Figure





**Figure 8.6. Percent of private, federal, and state land ownership within population seasonal ranges by sex and year for GPS-collared elk.**

8.9). The first was located along the Bitterroot River between Davis Creek and Woodchuck Creek. Movement patterns in this corridor run in two primary directions, NW-SE and NE-SW, and were completed by 19 collared individuals primarily during the archery and rifle hunting seasons during the morning (4–8AM) and evening (6–10PM). Paralleling and crossing the Bitterroot River, the NW-SE movements occurred between valley bottom riparian forests on private and state properties and grassland and agricultural areas on private properties at the toe of the adjacent foothills. The perpendicular NE-SW movements occurred between the valley bottom and higher elevation grassland and timbered foothills to the east. The second corridor was located on the north side of the middle reaches of Eightmile Creek with movements between agricultural areas and the higher elevation grassland and timbered foothills to the north. Movements in this corridor were completed by 16 collared individuals primarily during the late-summer, archery hunting, and rifle hunting seasons and typically in the evening (6–10PM). The third corridor was located south of the middle reaches of Ambrose Creek with movements between agricultural and riparian areas along the creek and the higher elevation grassland and timbered foothills to the south. Movements in this corridor were completed by 11 collared individuals primarily during the late-summer and archery hunting season and in the mornings (4–6AM) and evenings (6–10PM). The fourth corridor was located north of the middle reaches of Burnt Fork with movements between agricultural and riparian areas along the creek and the



**Figure 8.7. Percent of vegetation cover type within population seasonal ranges by sex and year for GPS-collared elk.**

higher elevation grassland and timbered foothills to the north. Movements in this corridor were completed by 20 collared individuals primarily during the late-summer and archery hunting season and between 6PM and 8PM. The fifth corridor was located south of Burnt Fork with movements between agricultural areas and grassland foothills to the southeast. Movements in this corridor were completed by 14 collared individuals primarily during the late-summer and archery and rifle hunting seasons in the mornings (4–6AM) and evenings (6–10PM).

We identified 59 instances of road crossings across US Highway 93 from 4 female and 2 male GPS-collared elk (Figure 8.10). Of these crossings, 33 occurred during the 2014 season with 3 during the summer (2 individuals), 2 during archery season (1 individual), 14 during rifle season (4 individuals), and 14 during winter-spring (4 individuals). There were 26 crossings during the 2015 season, with 1 during the summer, 12 during archery season (2 individuals), 2 during rifle season (1 individual), and 12 during winter-spring (3 individuals). All crossings occurred between 6PM and 6AM, with 78% occurring between 10PM and 2AM. Fifty-one percent were east to west crossings, reflecting a repetitive back-and-forth behavior of individuals through time. There were 5 instances where the same individuals re-crossed the highway within 2 hours of having crossed previously. All females that made crossings had annual distributions that ex-



**Figure 8.8. Percent of areas accessible and restricted to public hunting within population seasonal ranges by sex and year for GPS-collared elk.**

tended adjacent to and west of US Highway 93 and made rare, occasional crossings to and short stays on the east side of the highway. One female made 34 such crossings, accounting for 58% of the total crossings, spanning all seasons. This female occasionally re-crossed within the same day or by the following day, likely reflecting forage-related movements.

The two male elk that made crossings were more itinerant. One 2-year old male elk spent February to May 2014 on the east side of the highway, primarily near the Threemile Wildlife Management Area, crossed the highway once, and spent June to November 2014 on the west side of the road, primarily north of Sweeney Creek, where he was harvested. The second male, a 3-year-old elk, crossed 4 times; from February to April 2015, the male spent most of his time in the Davis Creek drainage and along the Bitterroot River riparian areas east of the highway, after which the elk crossed the highway and spent 9 days around McClain Creek before re-crossing to the east side. For most of May to September, the male was up Davis and Miller Creeks, then crossed to the west side back to McClain Creek for one month before returning to the Bitterroot Valley riparian areas through November where he was harvested.

All crossings occurred south of Lolo and north of Florence, between mile markers 78 and 83. Approximately 60% of the crossings occurred along a 1.3 km stretch of US Highway 93, about 1.7 km south of Lolo, between mile markers 81 and 83. The remaining occurred along on

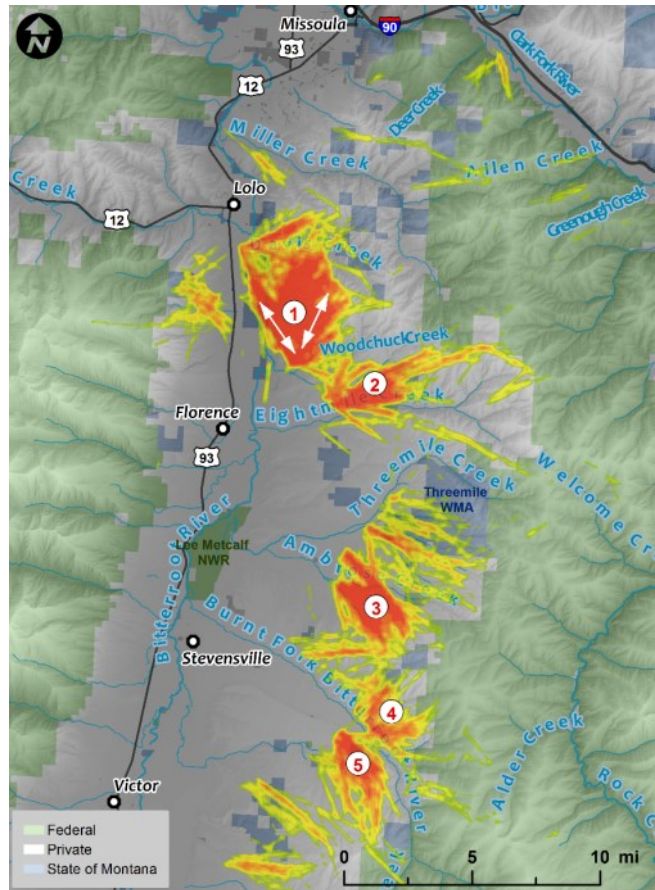
a 3 km stretch of US Highway 93, about 4.4 km south of Lolo, between mile markers 78 and 81. One collared female elk was killed by a vehicle on 26 December 2014 (see Section 7). She had made 6 previous crossings between 28 October and 14 November 2014.

## Discussion

The North Sapphire elk population demonstrated a variety of movement strategies that varied by season, sex, and individual. Generally, the population showed typical migratory characteristics (e.g., the female represented in Panel A, Figure 8.11) with movements from low elevation areas on primarily private lands to higher elevation areas on or adjacent to federal lands during the calving and summer seasons; however, a portion of the female population remained resident on the winter range year-round. Male elk used a higher proportion of coniferous forests and federal lands with steeper slopes and higher canopy cover as compared to female elk. Following the calving and summer seasons, the transition to archery and rifle seasons corresponded to distributional shifts to localized

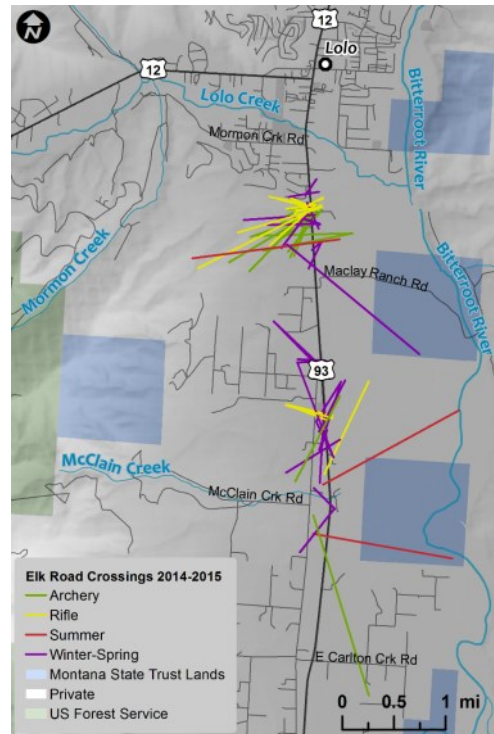
lower elevation private lands. Both female and male elk made these movements and generally used the same areas as expected from breeding biology and hunting pressure. Hunting pressure occurred on both species during this study, with harvest of brow-tined bull or antlerless elk permitted during the archery season and of brow-tined bull elk (with a general license) and antlerless elk (on limited B licenses and youth hunt general licenses) during the rifle season. There was an estimated average of 7,205 hunter-days per year during this study according to annual MFWP harvest surveys. During the rifle season, distributions of both sexes overlapped considerably. This apparent trade-off between acquiring nutritional resources that are only available during the summer-fall period and increasing security from harvest mortality may have consequences to the nutritional condition and, ultimately, the survival and reproduction of elk (see Section 10).

In contrast to the migratory movement strategy, a portion of the population demonstrated non-migratory movement strategies and remained at lower elevations throughout the year (e.g., the female represented in Panel B, Figure 8.11). These residents, the vast majority of which were female elk and generally located south of Lolo and north of Eightmile Creek, have

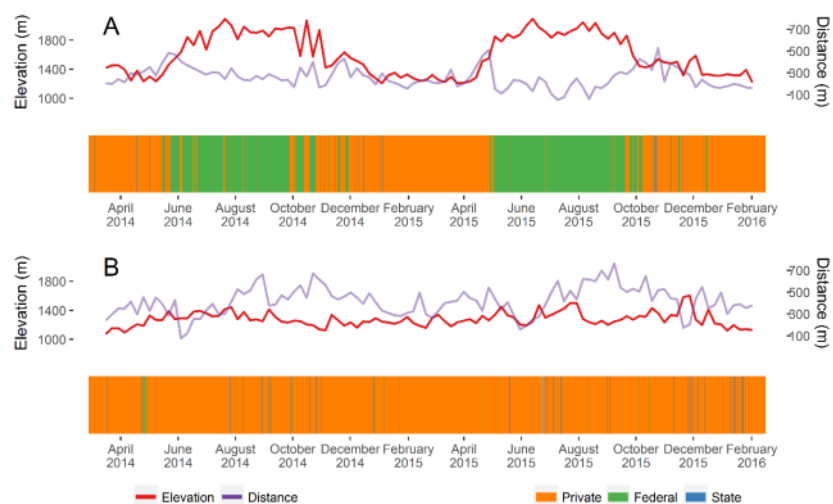


**Figure 8.9.** Travel corridors as identified by density of rapid, long distance movements (>2,500 m per 2 hours) by at least one individual across 2014-2015. Yellow to red indicate increasing densities of these movements through time. Red numbers indicate corridors discussed in text.

apparently foregone movement to resources at higher elevation areas during the summer. Irrigated agricultural areas provide important opportunities for resident elk to acquire nutritional resources during the summer (see Section 5). Some of the quick, long distance movements identified by our corridor definition reflect responses to harvest risk and acquisition of forage. These movements were often daily, back-and-forth patterns and strongly associated with hunting pressure from early- and late-season game damage hunts and the general hunting season on private property. Beginning around dusk, elk moved to take advantage of forage resources on irrigated agricultural areas. By dawn, the elk transitioned to less visible, higher security areas such as valley bottom riparian areas, adjacent foothills, or properties with restricted hunting. These resident elk can pose difficulties for private landowners, wildlife managers, and hunters due to increased private property damage, lack of accessibility and opportunity for harvest on public land, and inability to effectively reduce or stabilize the population with harvest. Loss of traditional migratory strategies by elk in the North Sapphire population is a concern and may present wildlife management difficulties, or potentially have consequences to the nutritional condition of the elk (see Section 9).



**Figure 8.10.** US Highway 93 seasonal crossings of GPS-collared elk during 2014–2015. Lines are segments connecting locations recorded prior to and after crossing the highway.



**Figure 8.11.** Time-scapes from GPS-collared elk illustrating examples of individual variation in movement and landscape use through time. Panel A: typical migratory elk (female). Panel B: typical non-migratory, resident elk (female).



## Section 9 — Nutritional Consequences of Varying Elk Migratory Behaviors

### Introduction

Partial migration, in which some individuals in a migratory population remain resident on a shared range year-round, is the most common form of migratory behavior in ungulates (Chapman et al. 2011). The timing, duration, and distance of migratory movements can vary widely within partially migratory populations (Boyce 1991, Luccarini et al. 2006, Mysterud 2013). Some individuals exhibit intermediate behaviors that lie somewhere between migration and residency, such as making multiple trips between distinct areas within the same season (Damiani et al. 2015). This wide variation in behavior suggests partial migration comprises a continuum rather than a simple dichotomy of resident vs. migratory behaviors. Although many studies have compared benefits of migration and residency in partially migratory populations, relative benefits of intermediate behaviors remain largely undescribed (Cagnacci et al. 2011)

Elk that exhibit different migratory behaviors typically occupy different portions of the population range during summer. Migrants move from low elevation winter range during spring, following the growth of highly nutritious emergent vegetation as it proceeds uphill into higher elevation summer range areas (Bischof et al. 2012). Residents remain in low elevation valley bottom areas throughout the year. Different land cover types associated with high elevation summer range and low elevation winter range support different species of plants, likely providing different nutritional resources to elk. The quality of forage available across the population range varies widely (see Sections 5 and 6), and exposure to nutritional resources during summer may differ for animals exhibiting different migratory behaviors. Because of the strong effect of summer nutrition on reproductive and survival rates of elk (see Section 5), elk that are exposed to different amounts of nutrition during summer may also exhibit different vital rates that could affect population demographics and distributions.



The North Sapphire elk population is partially migratory, with individual behaviors ranging across a continuum from migration to residency. Because migratory elk move to take advantage of high quality forage, exposure to high quality nutrition is typically considered a primary benefit of migration (Fryxell et al. 1988). In the North Sapphire Mountains, however, portions of elk winter range may also provide high quality nutrition during summer. Valley bottom areas include irrigated agricultural fields that resident elk use throughout the year. The corn and alfalfa grown in these fields can provide high quality nutrition, but it is unclear whether, and to

what extent, the nutrition available on these irrigated pastures may differ from the nutrition available on typical higher-elevation summer range. Because both migrant and resident behaviors in this area could feasibly expose animals to high quality nutrition, we tested the hypothesis that all types of migratory behaviors provide equivalent access to nutritional resources for elk in the North Sapphires. Specifically, we predicted the forage quality that adult female elk were exposed to during summer would not differ among resident, intermediate, and migratory elk.

## Methods

We chose forage quality (i.e., DE; see Section 5) as a measure of nutrition because it has been explicitly linked to reproductive and survival rates in elk (Cook et al. 2004, 2016). To estimate forage quality across the study area, we used the same methods described in Section 5 to create a predictive DE model specific to the North Sapphires. For the North Sapphire-specific model, we defined forage plants using only the summer diet data from the North Sapphire population, and we built the model using only data from North Sapphire vegetation plots.

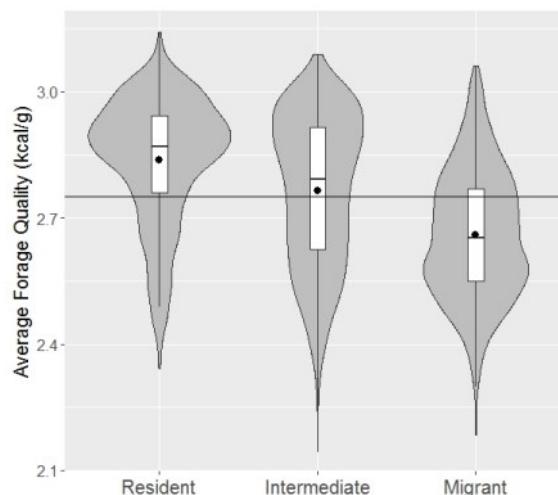
Using GPS collar location data from adult female elk, we classified individual behavior as resident, intermediate, or migrant by measuring volume intersection of kernel seasonal home ranges (i.e., utilization distributions; UD<sub>s</sub>) estimated from summer (Jul–Aug) and winter (Feb–Mar) location data (Fieberg and Kochanny 2005). We estimated home ranges (95% UD<sub>s</sub>) and core use areas (50% UD<sub>s</sub>) within each individual's seasonal home ranges. We defined migrants as individuals whose seasonal home ranges did not overlap (i.e., volume intersection of 95% and 50% UD<sub>s</sub> = 0). We defined residents as individuals whose core use areas overlapped (i.e., volume intersection of 50% UD<sub>s</sub> > 0). We considered all other animals to be intermediates (i.e., volume intersection of 50% utilization distribution = 0, volume intersection of 95% utilization distributions > 0). We also classified migratory behaviors along a continuum by ranking individuals first by the amount of intersection between core use areas, then by the amount of intersection between home range areas, such that lower intersection values indicated stronger migratory behavior. Individuals with volume intersection values of 0 were further ranked by Euclidean distance between centroids of seasonal home ranges, such that higher distances indicated stronger migratory behavior.

To assess nutritional consequences of differing migratory behaviors, we extracted predicted DE values associated with locations for each individual during summer. For this analysis we defined summer as July 15–August 31 to match the timing of vegetation sampling. We removed locations recorded during the warmest times of day (1400h–1800h) when elk were more likely to be resting than actively foraging (Merrill 1991). First, we calculated the mean DE each individual was exposed to each day during the summer. Second, we calculated the number of total days each individual was exposed to adequate ( $DE \geq 2.75$ ), marginal (2.40–2.75 DE), and poor ( $DE \leq 2.40$ ) forage quality throughout the summer. Results report mean  $\pm$  standard deviation of these values. We used analysis of variance (ANOVA) with post-hoc Tukey tests to test for differences between mean daily DE exposure, and between the number of days' exposure to adequate forage quality, for residents, intermediates, and migrants.

## Results

We estimated seasonal home ranges and core use areas for 46 adult female elk in 1 or 2 years resulting in a total of 75 elk-years. We defined 25% as residents ( $n = 19$ ), 48% intermediates ( $n = 36$ ), and 27% migrants ( $n = 20$ ). Residents composed 26.3% and 24.0% of the population in 2014 ( $n = 38$ ) and 2015 ( $n = 37$ ), respectively. Intermediates composed 47.4% and 49.0% of the population in 2014 and 2015, respectively. Migrants composed 26.3% and 27.0% of the population in 2014 and 2015, respectively. On average, summer home range sizes were  $68.5 \pm 26.3 \text{ km}^2$  for residents,  $63.8 \pm 20.3 \text{ km}^2$  for intermediates, and  $35.6 \pm 22.8 \text{ km}^2$  for migrants. Volume intersection between winter and summer home ranges (i.e., 95% UD) across all elk-years ranged from 0 to 42%. Volume intersection between winter and summer core use areas (i.e., 50% UD) ranged from 0 to 18%.

On average, residents were exposed to  $2.84 \pm 0.15 \text{ kcal/g}$  of digestible energy during summer, intermediates were exposed to  $2.77 \pm 0.18 \text{ kcal/g}$ , and migrants were exposed to  $2.66 \pm 0.15 \text{ kcal/g}$ . Migratory behavior groups varied in both the average forage quality they were exposed to each day ( $F_{2,72} = 12.58$ ,  $P \leq 0.001$ ) and in the number of days they were exposed to adequate forage quality ( $F_{2,72} = 15.11$ ,  $P \leq 0.001$ ). Migrants were exposed to lower forage quality each day than residents ( $p\text{-adj.} \leq 0.001$ ) or intermediates ( $p\text{-adj.} = 0.003$ ), but daily forage quality did not differ between residents and intermediates ( $p\text{-adj.} = 0.068$ , Figure 9.1). On average, residents were exposed to adequate forage quality for  $37 \pm 10$  days, intermediates were exposed to adequate forage quality for  $27 \pm 16$  days, and migrants were exposed to adequate forage quality for  $13 \pm 11$  days during the 48-day summer period. Migrants were exposed to adequate forage quality for fewer total days than residents or intermediates (Figure 9.2;  $p\text{-adj.} < 0.01$ ). Intermediates were exposed to adequate forage quality for fewer days than migrants ( $p\text{-adj.} = 0.001$ ); however, we found only weak evidence for differences between the average DE intermediates and residents were exposed to per day ( $p\text{-adj.} = 0.035$ ). The forage quality that migrants were exposed to was consistently lower than the forage quality intermediates or residents were exposed to throughout the summer; migrant daily nutritional exposure showed a general decreasing trend while resident and intermediate daily nutritional access exhibited stable or increasing trends throughout the summer (Figure 9.3). Average nutritional exposure decreased monotonically across the continuum from residency to migration (Figure 9.4).

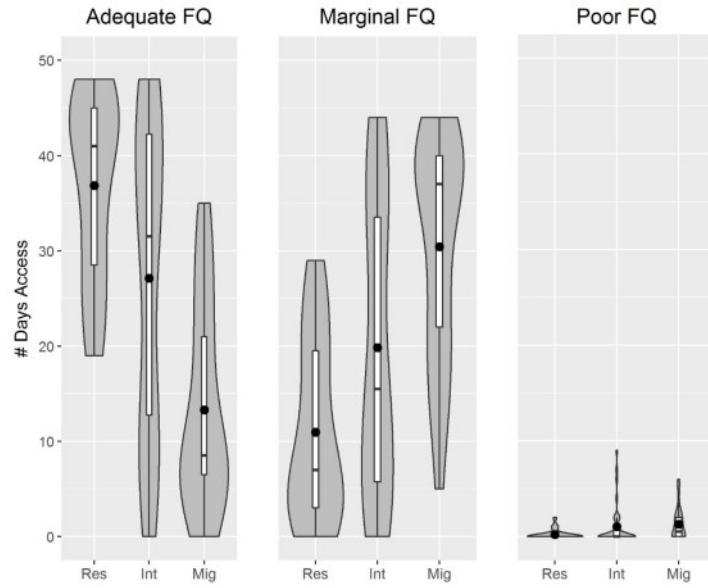


**Figure 9.1.** Violin plots showing the average forage quality (kcal of digestible energy/g of available forage) adult female elk exhibiting resident, intermediate, and migratory behaviors were exposed to during summer (Jul 15-Aug31) 2014 and 2015. Black dots represent mean values. The horizontal line represents adequate forage quality ( $\geq 2.75 \text{ kcal/g}$ ). Violin plots combine traditional box-and-whisker plots (white) representing the 5-number summary (minimum, first quartile, median, third quartile, and maximum) with kernel density estimates (gray) representing a mirrored probability density of the data.

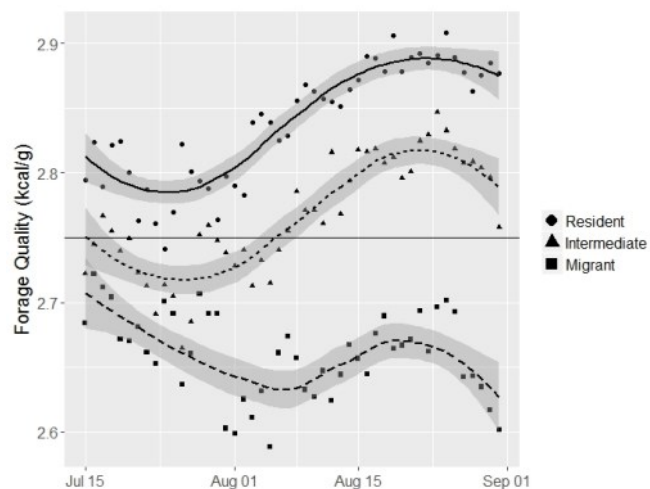
## Discussion

Contrary to our prediction that all migratory behaviors provided elk equivalent nutritional exposure, we found migrants were exposed to lower forage quality than residents or intermediates during summer. Forage quality exposure decreased along the continuum from resident to migratory behavior, indicating resident individuals that moved the least between winter and summer ranges had access to the highest quality summer forage. Additionally, results suggest intermediate behaviors did not represent a “middle ground” providing nutritional benefits that were intermediate between those of residents and migrants. Rather, nutritional benefits of intermediate behaviors were more similar to those of residents than of migrants. We found strong evidence for differences in nutritional exposure between migrants and intermediates but very weak evidence for differences between intermediates and residents. The forage quality migrants were exposed to, though lower than that of residents and intermediates, was not predicted to be low enough to affect survival (Cook et al. 2004, 2016); however, the differences in nutritional resources across the migratory and resident summer ranges have the potential to strongly influence elk distributions and affect migratory behaviors.

Our results indicate a strong influence of irrigated agricultural lands on nutritional exposure of elk during summer. Irrigated agricultural areas provided the highest DE ( $3.12 \pm 0.16$  kcal/g) of all 12 land cover types



**Figure 9.2.** Violin plots showing the number of days adult female elk exhibiting resident (Res), intermediate (Int), and migratory (Mig) behaviors had access to adequate ( $\geq 2.75$  kcal/g), marginal ( $2.40\text{--}2.75$  kcal/g), and poor ( $< 2.40$  kcal/g) forage quality (FQ) during summer (Jul 15–Aug 31) 2014 and 2015. Black dots represent mean values. Violin plots combine traditional box-and-whisker plots (white) representing the 5-number summary (minimum, first quartile, median, third quartile, and maximum) with kernel density estimates (gray) representing a mirrored probability density of the data.

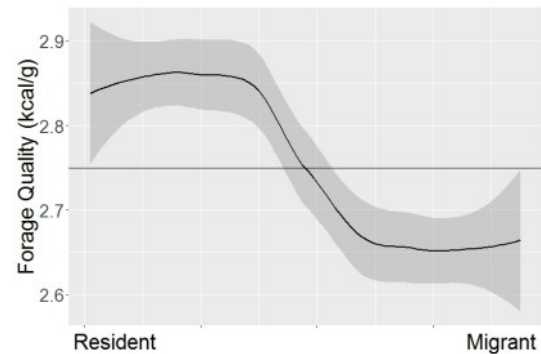


**Figure 9.3.** Daily forage quality exposure for resident, intermediate, and migratory elk in a partially migratory population in the North Sapphire Mountains, Montana, USA during summer 2014 and 2015. The horizontal line represents adequate forage quality ( $\geq 2.75$  kcal/g).

in the study area. Resident elk in the North Sapphires, in addition to being exposed to the highest quality forage, were also located in irrigated agricultural land for the most total days during summer (30 days on average, as opposed to 19 days for intermediates and only 2 days for migrants). Despite the fact that all land cover types in this area other than late-successional wet forests can provide, on average, adequate nutrition for elk during summer, the extremely high nutritional quality of irrigated agricultural lands still provides a strong draw for elk to remain resident in valley bottom areas throughout the year. Thus, where elk winter range is converted to irrigated agricultural land, increasing proportions of the population may forego traditional seasonal migration to higher elevation summer range.

Relative to other mountain ranges in the region, the North Sapphires lie at relatively low elevation, with no peaks occurring above tree line. This area lacks an abundance of alpine grasslands that serve as traditional summer range for many migratory elk. The relative effects of irrigated agricultural lands and alpine grasslands on elk nutritional exposure during summer remain unclear and may have a strong effect on relative nutritional exposure of elk with different migratory behaviors in other partially migratory populations.

Previous work has shown that changing climate and land use practices have altered, reduced, or resulted in complete loss of migratory behavior for large herbivores worldwide (Berger 2004, Bolger et al. 2008, Harris et al. 2009). Our results demonstrate a strong link between land use practices and elk migratory behaviors in the North Sapphires. Though some work indicates loss of migratory behavior can result in population declines, our work suggests increased resident behavior in partially migratory populations does not always negatively affect population vital rates. Data gathered during elk capture indicates the population is in generally good health (see Section 4). Changing migratory behaviors can affect other species, however, in areas where migrations have traditionally occurred (Wilcove and Wikelski 2008). For instance, migratory ungulates can play an important role in nutrient cycling via herbivory and fecal depositions (Schoenecker et al. 2004), and they often serve as important prey species for carnivores during summer (Merkle et al. 2009, Metz et al. 2012). Additionally, loss of traditional migratory behaviors may result in increasing property damage issues on private lands and lack of availability of elk on higher elevation public lands during the fall hunting season.



**Figure 9.4.** Average daily forage quality available to elk during summer decreases monotonically with increasing strength of migratory behavior in the North Sapphire Mountains, western Montana, USA, 2014-2015. The horizontal line represents adequate forage quality ( $\geq 2.75$  kcal/g). We placed individuals along this behavioral continuum by ranking them first by the amount of core use area (50% kernel density estimator) volume intersection, then by the amount of home range (95% kernel density estimator) volume intersection, such that higher intersection values indicated stronger resident behavior. Individuals with no volume intersection between home ranges were further ranked by Euclidean distance between home range centroids, such that higher distance values indicated stronger migratory behavior.



## Section 10 — The Effect of the Archery Season on Elk Habitat Selection

Montana's archery hunting season may influence elk fall habitat selection and distributions as elk act to reduce the risk of harvest mortality (Conner et al. 2001, Vieira et al. 2003, Cleveland et al. 2012, Ranglack et al. 2017). This behavioral strategy may have consequences to ungulate nutritional condition and ultimately survival and reproduction, if access to higher quality nutritional resources is limited or reduced as animals alter movements to reduce harvest risk (Cook et al. 2004, 2013, Hebblewhite 2006, DeCesare et al. 2014). Elk may select areas of higher nutritional quality when risks of using those areas are low (Pyke 1984, Ferrari et al. 2009), and they may select security areas of inferior nutritional quality when mortality risk increases (Hernández and Laundré 2005, Hebblewhite and Merrill 2009). These security areas typically



provide physical hiding cover that obscures the animal from view or allows it to swiftly escape danger (Skovlin et al. 2002). Additionally, areas with restricted access for public hunting may provide important security opportunities for elk (Proffitt et al. 2016c, Ranglack et al. 2017). Preferential selection of elk for security areas over higher quality forage can reduce direct mortality from harvest but may incur longer-term consequences to survival or reproduction through reduced nutritional condition (Cook et al. 2004).

Alternatively, in some landscapes, elk may be able to seek out areas of low harvest risk while maintaining access to high quality nutritional resources. The northern Sapphire Mountains in west-central Montana provide a matrix of publicly-owned elk habitat that allows for unrestricted hunter access adjacent to privately-owned valley bottom lands with varying degrees of restricted public hunter access. In addition, the availability of irrigated agricultural areas on this landscape provides high quality nutritional resources. These private properties that restrict public hunter access and allow elk access to high quality nutritional resources, may serve as refuge areas for elk. Such refuge areas may reduce the number of elk available for harvest on publicly accessible lands and limit the effectiveness of traditional harvest and population management strategies (Burcham et al. 1999, Haggerty and Travis 2006).

Understanding the role of the archery hunting season on elk distributions and acquisition of nutritional resources is valuable for developing elk harvest and habitat management plans. This may become more relevant to elk managers given the continued increase in the popularity of archery hunting, with a 98% increase in archery hunting license sales since 1985 in Montana (Montana Fish, Wildlife and Parks, unpublished data). Our primary objective was to evaluate the effect of archery hunting on female elk resource selection and assess the potential trade-offs between acquiring nutritional resources and minimizing mortality risk across a diverse landscape of variable nutritional resources, security, and refuge availability. We focused

on testing the hypotheses that: 1) the archery season limits elk ability to access higher quality nutritional resources as elk prioritize selection of areas providing increased security, and 2) on diverse, human-altered landscapes, the archery season does not constrain the ability of female elk to access higher quality nutritional resources as elk can select refuge areas providing both increased security and forage. We tested these predictions using two years (2014–2015) of GPS locations collected from female elk.

## Methods

We limited the elk location data (see Section 8) in this analysis to a pre-archery (i.e., 1 month prior to the start of archery season) and an archery (i.e., Sept. 5–Oct. 20, 2014 and Sep. 4–Oct 19, 2015) period. We evaluated individual elk selection for locations within the population home-range based on a used-available design (i.e., Design II; Manly et al. 2002) that represents selection somewhere between second- and third-order (Johnson 1990). We chose this method because our primary purpose was to understand population-level selection where the entire population home-range was available to individual elk. We randomly generated available points at a ratio of 1:5 (used:available) within the extent of the population's seasonal range, which we defined using a 95% kernel density estimator contour that encompassed both the pre-archery and archery periods.

We evaluated the effect of 8 covariates potentially affecting female elk resource selection: land cover type, slope, distance to cover, distance to motorized road, security patch, hunter access, archery period, and forage quality. We classified land cover types into 3 categories: forests, montane riparian, and valley bottom habitats (grasslands, shrublands, riparian, and agricultural areas). We defined cover as areas with forest canopy cover  $\geq 40\%$  (Proffitt et al. 2016c). We defined motorized roads as routes open for motorized travel as designated during each pre-archery and archery period. We developed multiple variants of the binary security patch covariate representing roadless areas of a given size ( $\geq 100, 500, 1000, 1500$  ha), distance to the nearest motorized road ( $\geq 0.4, 0.8, 1.2, 1.6$  km), and canopy cover ( $\geq 0, 10, 30, 50\%$ ) making up greater than 75% of the roadless area. Current National Forest management plans incorporate the definition of  $\geq 100$  ha of continuous forest located  $\geq 0.8$  km from the nearest road open to motorized travel during the hunting season (Hillis et al. 1991, Christensen et al. 1993). We classified hunter access into 2 categories: accessible to public hunting and restricted public hunting access. Areas of restricted public hunting access included private lands that allowed for hunting without a fee to only family and friends, or through any other system that restricted free, unlimited public access. We classified the archery period variable into a pre-archery and archery period as defined by the dates of the hunting season. We estimated forage quality (i.e., digestible energy per gram of forage, kcal/g) based on extensive elk diet and vegetation surveys collected during late summer (see Section 5).

We evaluated factors affecting elk resource selection using general linear models with a binomial distribution based on the used and available locations. We first pooled used and available locations for all individuals in a multi-tiered modeling approach to arrive at a best-supported population-level model and fit this model to each individual's set of used and availa-

ble locations to estimate individual-level selection coefficients. We then quantified the population-level resource selection by averaging selection coefficients across individuals.

## Results

We retrieved radio-collar location data from 41 female elk over 1 to 2 years for a total of 74 individual elk-years. After constraining the data to the pre-archery and archery periods for use in this analysis, we retained 26,745 locations, or an average of 652 locations per elk (range 255–735).



During the pre-archery period, a greater proportion of locations were found in forests and within areas accessible to public hunting and a smaller proportion were located in valley bottom habitats as compared to the archery period (Table 10.1). Locations averaged further from roads, closer to cover, and lower forage quality during the pre-archery period as compared to the archery period. Prior to the archery period, the average forage quality of female GPS locations found in areas

restricting public hunting access was  $2.88 \pm 0.13$  kcal/g (SD) and in areas accessible to public hunting was  $2.69 \pm 0.17$  kcal/g. During the archery period, the average forage quality in areas restricting public hunting access was  $2.89 \pm 0.13$  kcal/g (SD) and in areas accessible to public hunting was  $2.68 \pm 0.18$  kcal/g.

**Table 10.1. Summaries of used locations for evaluating female elk resource selection during the pre-archery and archery period.**

Summary	Pre-archery	Archery
Percent in forests	54	42
Percent in valley bottom habitats	41	53
Percent in montane riparian	5	5
Percent in publicly accessible areas	53	36
Mean ( $\pm$ SD) distance to roads (m)	1,017 $\pm$ 952	975 $\pm$ 841
Mean ( $\pm$ SD) distance to cover (m)	157 $\pm$ 235	210 $\pm$ 293
Mean ( $\pm$ SD) forage quality (kcal/g)	2.78 $\pm$ 0.18	2.81 $\pm$ 0.18

Our population-level model included land cover type, quadratic slope, hunter access, distance to cover, distance to motorized road, forage quality, archery period, and interaction terms of archery period  $\times$  hunter access, archery period  $\times$  distance to cover, archery period  $\times$  distance to motorized road, and archery period  $\times$  forage quality. We fit this model to each individual female elk and averaged the standardized coefficient estimates (Table 10.2). The averaged coefficients indicated that female elk selected for areas that restricted public hunter access, areas further from cover, and areas further from motorized roads during the pre-archery periods. During the archery period, selection for areas that restricted public hunter access and areas further from motorized roads was stronger during the archery period (Figure 10.1). Female elk also selected for areas further from cover during archery period. Female elk selected for areas with higher forage qual-

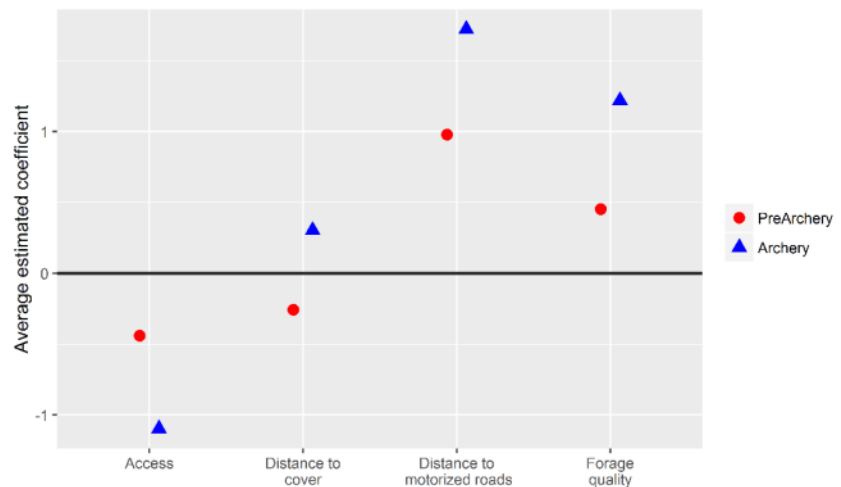
**Table 10.2. The averaged standardized coefficients and 95% confidence intervals (LCI=lower, UCI=upper) representing the population-level effects of covariates on female elk resource selection during the fall.**

Variable	Average	SE	LCI	UCI
Intercept	-2.46	0.23	-2.9	-2.01
Valley Bottom Habitat	-0.09	0.07	-0.23	0.05
Montane Riparian	-0.97	0.14	-1.24	-0.7
Slope	-0.43	0.07	-0.57	-0.3
Slope <sup>2</sup>	-0.15	0.08	-0.32	0.01
Access	-0.44	0.36	-1.15	0.27
Forage Quality	0.45	0.09	0.28	0.63
Distance to Cover	-0.26	0.07	-0.39	-0.12
Distance to Motorized Road	0.98	0.27	0.45	1.51
Archery	0.66	0.21	0.25	1.07
Access × Archery	-1.32	0.26	-1.84	-0.8
Forage Quality × Archery	0.1	0.08	-0.04	0.25
Distance to Cover × Archery	-0.1	0.06	-0.23	0.02
Distance to Motorized Road × Archery	0.08	0.14	-0.2	0.36

ity during both the pre-archery and archery periods, and selection for higher forage quality was stronger during the archery period. Female elk selected for forests over montane riparian and valley bottom habitats and for optimal slopes.

## Discussion

We found support for our hypothesis that as female elk act to reduce mortality risk during the archery season, their ability to access higher quality nutritional resources is not constrained. Our results indicated that female elk in the North Sapphire population responded to the increased mortality risk of the archery season by primarily selecting for areas with restricted public hunting access, closer to cover, and further from motorized roads. Selection for areas closer to cover may indicate that female elk were responding to the increased risk of mortality by selecting for areas with higher visibility in order to detect hunters.



**Figure 10.1. Averaged estimated coefficients demonstrating the effect of the archery hunting season. Values for the archery hunting season include the coefficient estimates for the archery variable and interaction terms.**

While female elk selection for all variables describing security areas (i.e., restricted public hunting access, closer to cover, and further from motorized roads) was greater under the increased mortality risk of the archery season, selection for areas of higher forage quality was also greater during the archery season. Increased use of areas with higher quality nutritional resources may be due to the combination of good nutrition and increased security on private lands that have variable vegetation cover types. Irrigated agricultural areas may be particularly important and contained approximately 2-4 times the forage quality than mature dry coniferous forests and open grasslands/shrublands in this landscape (see Section 5). Where public hunting access is restricted, either on or adjacent to agricultural areas, these areas may attract elk due to the combination of both security from harvest mortality and access to nutritional resources. In our study area, areas restricting public hunting access had higher quality forage ( $\bar{x} = 2.89$  kcal/g) that may better meet female elk nutritional requirements as compared to areas with public hunting access ( $\bar{x} = 2.68$  kcal/g). While the availability of forage quality does not represent actual nutritional intake by an animal, female elk on areas restricting public hunting access were predominantly exposed to levels of forage quality considered good (2.75–2.89 kcal/g; minor nutritional limitations on reproductive and survival performance) to excellent ( $\geq 2.90$  kcal/g; no nutritional limitations) for lactating female elk in summer and early autumn (Cook et al. 2004, 2016). Female elk on areas accessible to public hunting were predominantly exposed to levels of forage quality considered marginal (2.40–2.74 kcal/g; significant limitation on reproductive and survival performance) to good.

Prior to the archery period, female elk were also exposed to different levels of forage quality on areas restricting public hunting access ( $\bar{x} = 2.88$  kcal/g) and accessible to public hunting ( $\bar{x} = 2.69$  kcal/g), similar to levels during the archery period. Female elk selection for areas restricting public hunting access prior to the archery period may be due to these properties offering greater availability of high quality forage or reduced mortality risk from carnivores given proximity to human activities. However, given low wolf activity in the study area and no evidence of carnivore predation of collared elk during this study, it is likely female elk were selecting areas restricting public hunting primarily to acquire the nutritional resources provided on those properties. The availability of high quality forage on these properties prior to and during the hunting seasons likely provide elk with opportunities to satisfy survival and reproductive requirements. Our study on migration (see Section 9) lends support to this, showing that about 25% of the female elk in this population were non-migratory and resided on private properties yearlong. It is unknown whether this non-migratory strategy represents a long-term behavioral adaptation (Boyce 1991) or a shorter-term response to harvest pressures and/or an altered availability of nutritional resources on the human-modified landscape (Millspaugh et al. 2000), but it suggests that resident female elk may be fulfilling life-history requirements by utilizing the security and forage resources that are provided by these restricted public access properties.

Elk selection for areas restricting public hunter access during the hunting season has been reported in other elk populations in Montana and the western United States (Burcham et al. 1999, Conner et al. 2001, Proffitt et al. 2010, 2013, 2016c, Ranglack et al. 2017). This elk distribution shift presents a major challenge to wildlife managers trying to manage increasing elk populations to within socially-acceptable numbers while providing hunter opportunity. The



North Sapphire population is currently at near-record counts and the combination of hunter pressure on public lands and hunter access restrictions are limiting the effectiveness of harvest regulations to reduce adult female survival and overall population growth to meet population objectives. Further increasing hunter opportunity on public lands to achieve sufficient harvest will be ineffective and may further strengthen selection for areas with restricted public hunter access. Strategies to reach a more uniform distribution of hunter pressure across both public and private lands by manipulating hunter access and harvest regulations on both land ownerships are key to managing elk on the North Sapphire landscape.

## Section 11 — Conclusions and Management Applications

The North Sapphire elk population counts are steadily increasing. In this study, we found high annual adult female survival rates ( $\bar{x} = 0.91$ , 95% CI = 0.82–0.96) and pregnancy rates ( $\bar{x} = 0.91$ , 95% CI = 0.83–1.0). Together with indices of adequate recruitment (22.3 calves per 100 adult females), these metrics indicate a healthy elk population with no evidence that predation, disease, or nutritional resources were limiting population growth. We found harvest-related activities to be the primary cause of mortality for both female ( $\geq 71\%$ ) and male ( $\geq 87\%$ ) adult elk.

Despite the evidence for a healthy and increasing elk population, both landowner and hunter survey respondents perceived there to be too few elk as compared to the past. This perception may be attributed to elk redistribution from public lands to private properties where they may be less visible to public land hunters and the majority of landowners, particularly during the fall hunting seasons. In addition, resident and intermediate-migratory elk using private properties may comprise approximately 25% and 50% of the population, respectively. Female elk used two general regions throughout the year but more strongly during the archery and rifle hunting seasons: 1) between Miller and Eightmile Creek, and 2) between Ambrose Creek and Burnt Fork. Both of these areas consisted primarily of undeveloped open grassland and shrubland habitats and dry coniferous forests with topographically complex mountain foothill terrain. Along the lower-elevation margin of these areas were irrigated agricultural lands, and many of the travel corridors we identified in this study reflect regular or daily movements between these irrigated agricultural areas and the higher elevation open habitats of the mountain foothills.



Our assessment of summer nutritional resources revealed that irrigated agricultural areas provided approximately 2–4 times higher forage quality and 10–20 times greater forage abundance than mature dry coniferous forests and open grasslands/shrublands, indicating that elk are likely satisfying nutritional requirements by taking advantage of the irrigated agricultural areas. These results were supported by our evaluation of migratory behaviors that found resident elk were exposed to adequate nutritional resources and spent on average 11

and 28 more days during the summer on irrigated agricultural areas as compared to intermediate migrant and migratory elk, respectively. The matrix of land cover types and restricted hunter accessibilities on the northern Sapphire landscape, particularly during the hunting seasons, appear to be ideal elk refuges providing both sufficient nutritional resources and security.

While we found evidence that nutritional resources were not limiting to the population as a whole, migratory elk were exposed to lower quality forage as compared to resident and

intermediate migrant elk. These migratory elk may be able to behaviorally compensate for being in areas of lower forage quality; however, this indicates high elevation summer ranges may not be able to support the same elk densities as lower elevation. Land managers may be able to enhance the nutritional capacity of high elevation summer ranges through habitat management actions (discussed below).

The annual male elk survival rate ( $\bar{x} = 0.46$ , 95% CI = 0.26–0.64) was similar to other harvested elk populations in Montana and other western states. The adult male survival rate, adequate recruitment rate in the population, and high observed ratio of males (18 bulls per 100 adult females) indicate that current levels of adult male harvest mortality are sustainable given current hunter opportunity in this population. Additionally, at least forty percent of harvested male elk and 45% of radio-collar locations during the hunting seasons occurred on public lands, indicating that hunter opportunity for male elk on public lands remains available.

Current elk population management strategies are primarily focused on reducing the population growth rate through increased antlerless licenses and providing male elk harvest opportunity. Past management actions of less restrictive regulations on antlerless harvest were effective in reducing the population size and increasing hunter opportunity. However, with the increased human development, reduced public hunter access on some key properties, and increased elk use of areas that restrict hunter access, the effectiveness of this harvest management strategy may now be limited. Based on our evaluations of nutritional resources, migratory behavior, and habitat selection, we recommend managers trying to decrease elk population numbers consider strategies integrating management of hunter access, habitat quality, and hunting regulations that are matched to the present migratory behaviors and distribution of female elk in the population. Broadly applying harvest management across the entire population may have unintended consequences to the migratory segment of the population, reducing variation in migratory behaviors which may ultimately exacerbate the problem of increased elk use of private property refuge areas, reduce hunter opportunity, and increase property damage of private landowners. While there is evidence for flexible and adaptive migration strategies in this population, knowledge of particular high elevation summer ranges used by individuals may be difficult to reintroduce back to the population once lost through mortality of these individuals.

Efforts to increase the nutritional capacity of summer ranges on public lands through improved forage quality and abundance may be an effective way to support a greater number of reproductively successful female elk employing migratory strategies and increase the attractiveness of these areas to resident elk. Our results indicate that strategic management of wildfires may be a useful method to affect the availability and distribution of nutritional resources. Elk and forest managers working in collaboration can identify areas where wildfire can be left to burn or suppressed to create a mosaic of burn histories that provide enhanced elk nutritional resources and adequate security cover. At lower-elevation areas occupied by resident elk, management focusing on limiting elk accessibility to nutritional resources on irrigated agricultural areas through collaborations with private landowners may be useful for reducing the ability of non-migratory elk to acquire adequate nutritional resources and encourage use of forage resources available on public land. Management strategies focused on increasing public hunter

access on private properties without concurrently reducing hunter pressure on public lands may not be effective in redistributing elk to public lands. Ultimately, collaborations with private landowners and development of strategies to reach a more uniform distribution of hunter pressure across the landscape are essential to reducing the elk population to within population objectives.



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